REVISION OF THE BLACK FLY GENUS *GIGANTODAX* (DIPTERA: SIMULIIDAE)

PEDRO WYGODZINSKY AND SIXTO COSCARÓN

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REVISION OF THE BLACK FLY GENUS *GIGANTODAX* (DIPTERA: SIMULIIDAE)

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ABSTRACT

A taxonomic study of the genus *Gigantodax* Enderlein is presented, including keys, descriptions, redescriptions, discussions, illustrations, and distributional and biological information. *Gigantodax* is the largest genus of Neotropical Prosimuliini, with 64 species extending along the Andean system from Mexico to Tierra del Fuego. Because most species described herein were collected by the authors from breeding sites, the morphology of immature and adult stages is presented. The species are tentatively arranged into eight groups as follows: (1) **cortesi** group; *G. cortesi* n. sp. (N Chile), *G. jatunchuspi* n. sp. (N Chile), *G. punapi* n. sp. (N Chile, NW Argentina, and Bolivia), *G. chacabamba* (Peru). (2) **igniculus** group; *G. carmenae* n. sp. (Patagonian Andes), *G. igniculus* Coscarón and Wygodzinsky. (3) **minor** group; *G. araucanius* (Edwards), *G. eremicus* n. sp. (N Chile), *G. minor* n. sp. (central Chile and Patagonian Andes), *G. bolivianus* Enderlein. (4) **multifilis** group; *G. multifilis* n. sp. (Ecuador). (5) **brophyi** group; *G. brophyi* (Edwards), *G. rufidulus* n. sp. (Patagonian Andes), *G. antarcticus* (Bigot), *G. trifidus* n. sp. (central Chile and Patagonian central Andes of Argentina), *G. femineus* (Edwards), *G. marginalis* (Edwards), *G. kuscheli* Wygodzinsky, *G. luispenai* n. sp. (central Chile), *G. chilensis* (Philippi), *G. flabellus* (Venezuela and Ecuador), *G. awa* n. sp. (east slope Peruvian Andes), *G. paramorum* n. sp. (Colombia), *G. viannamartinsi* Ramirez Perez, *G. ortizi* Wygodzinsky, *G. multituberculatus* n. sp. (Colombia and Ecuador), *G. patihuaycensis* n. sp. (east slope Peruvian Andes), *G. laevigatus* n. sp. (Ecuador), *G. zumbahuae* n. sp. (Ecuador). (6) **cilicinus** group (with three subgroups); subgroup A; *G. fulvescens* (Blanchard), *G. shannoni* (Edwards), *G. destitutus* n. sp. (Venezuela and Colombia), *G. basinflatus* n. sp. (Colombia and Ecuador), *G. mariobordai* n. sp. (Bolivia), *G. incomitatus* n. sp. (Venezuela); subgroup B; *G. pennipunctus* Enderlein; subgroup C; *G. arrarteorum* n. sp. (east slope Peruvian Andes), *G. cilicinus* n. sp. (central Andes of Argentina), *G. clandestinus* n. sp. (Ecuador). (7) **cormonsi** group; *G. gracilis* n. sp. (Ecuador), *G. misitu* n. sp. (Colombia and Ecuador), *G. brevis* n. sp. (Colombia), *G. wygodzinskyi* Moncada, de Hoyos, and Bueno, *G. leonorum* n. sp. (Ecuador), *G. abalosi* Wygodzinsky, *G. cormonsi* n. sp. (Peru), *G. praealtus* n. sp. (N Chile), *G. vulcanius* n. sp. (Ecuador), *G. siberianus* n. sp. (Colombia). (8) **wrighti** group (with two subgroups); subgroup A; *G. horcotiani* Wygodzinsky, *G. bettyae* Wygodzinsky, *G. septenarius* n. sp. (Venezuela and Colombia), *G. conviti* Ramirez Perez; subgroup B; *G. aquamarensis* De Leon, *G. cervicornis* Wygodzinsky, *G. corniculatus* Wygodzinsky, *G. wrighti* (Vargas, Martinez, and Diaz Najera), *G. nasutus* n. sp. (Colombia), *G. rufescens* (Edwards), *G. dryadicaudicis* n. sp. (central Chile and Patagonian Andes), *G. incapucara* n. sp. (Bolivia), *G. herreris* n. sp. (Peru and N Chile), *G. impossibilis* Wygodzinsky, and *G. cypellus* n. sp. (Ecuador).

The following new synonymies are recorded: *G. nigrescens* (Edwards) with *G. antarcticus* (Bigot), *G. rufinotus* (Edwards) with *G. chilensis* (Philippi), *S. philippianus* Pinto with *G. marginalis* (Edwards), and *G. bonorinorum* Coscarón and Wygodzinsky with *G. brophyi* (Edwards).

INTRODUCTION

In a previous work (Wygodzinsky and Coscarón, 1973) the 14 species of eight of the nine genera of the Prosimuliini (sensu Crosskey, 1969) of Mesoamerica and South America were described and keyed. Those of *Gigantodax,* which we are revising herein, were excluded.

Each of these eight genera, with a total of 17 species now known, has a distribution restricted either to southern Mexico and Central America, central Chile, or southern Chile and Argentina. *Gigantodax* is distributed along the Andes from southern Mexico to Tierra del Fuego, with the number of species now being 64.

MATERIAL AND METHODS

In general the same characters are used to separate the species of *Gigantodax,* sometimes with more emphasis on morphological variation or certain meristic characters. Ratios are useful to differentiate some species, especially when the adults are otherwise very homogeneous in external appearance, without notable patterns of ornamentation and with limited differences in genitalic morphology. Some of the adults are difficult and/or sometimes impossible to separate, even when using microscopic characters and measurement ratios. The larvae have better char-

acters but some species still cannot be distinguished. Fortunately, the pupae possess useful characters, especially in gill morphology. The extraordinary variation of the pupal gills found among species of *Gigantodax* is unique in the Simuliidae. It was necessary to define some species by using a combination of characters from each life stage.

The keys reflect difficulty in finding good characters to separate species in all stages. In the keys, the geographical distribution is noted after the description of each species.

The species treatments are arranged in groups, most of which are well defined by apomorphic characters. The reader is referred to our above-cited work for a description of terms used herein. We neither formally name supraspecific taxa nor use as subgenera available names such as *Archinesia*. *Archinesia* is based on *Gigantodax femineus* which is an atypical species.

Most specimens were collected by the authors and reared in individual vials. Some were borrowed from the institutions listed below. The drawings were made with the aid of a camera lucida. Measurements were made with the use of an ocular micrometer.

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Most illustrations were made by the authors, Miss E. Buono, and N. Caligaris. Miss Linnae contributed some drawings, which bear her signature.

Abbreviations

AMNH	American Museum of Natural History
BMNH	R. W. Crosskey, British Museum (Natural History), London
CAS	P. H. Arnaud, Jr., California Academy of Sciences, San Francisco
CIS	E. I. Schlinger, California Insect Survey, University of California, Berkeley
CNC	Canadian National Collection, D. M. Wood, Biosystematics Research Institute, Agriculture Canada, Ottawa
IML	A. Willink, Instituto Miguel Lillo, Tucuman, Argentina
INM	A. Bachmann, formerly of Instituto Nacional de Microbiology, Buenos Aires, Argentina
ISET	A. Diaz Nájera, Instituto de Salubridad y Enfermedades Tropicales, D. F. México
MHN	G. Kuschel, formerly of Museo de Historia Natural, Santiago, Chile
MLP	Museo de La Plata, Argentina
USNM	F. C. Thompson and B. V. Peterson, National Museum of Natural History, Smithsonian Institution, Washington, D.C.
UCH	R. Cortes and L. Pena, Universidad de Chile, Santiago, Chile

Distribution and Habitat

Members of the genus *Gigantodax* are found in temperate and alpine habitat from central Mexico to Tierra del Fuego. They have been found from sea level at high latitudes to 4700 m in the tropics, but they generally prefer altitudes from 700 to 2000 m. Some species such as the Patagonian *igniculus* or *rufescens* live at 1800 m in the northern Patagonian Andes, but at sea level to 2000 km to the south. *Gigantodax brophyi* lives at the same localities, but in the north it occurs at a lower elevation (800 m) where it emerges in early spring (October).

Gigantodax adults and larvae live at temperatures from near 0 to about 25°C. Sometimes they must tolerate this temperature range in the same day, because of day-night temperature variations at high altitudes. Such change is especially characteristic of small streams that are the preferred habitats. In some places, like the Puna area, the borders of streams may be frozen from sunset until

morning. In the high mountains or in southern areas the species pass most of the winter under the snow.

Larvae and pupae can live in rivulets or streams as well as rivers, although they prefer small or fast-flowing streams. They can live in crystalline to muddy waters that have abundant sediment. Small streams with slow currents and abundant diatoms generally have only *Gigantodax* species. The preferred pH is about 7, but some species can live in acid water that crosses peat deposits or in very alkaline water that crosses borax deposits.

The adults are not anthropophilic. Some information suggests that they feed on the blood of birds, which we have not observed.

Distributions of the species groups are given in the maps (figs. 13, 32, 80, 109, 137, 177). The *cortesi* group is restricted to altitudes over 3000 m in the high plateau of the "puna" region. The *igniculus* group is found on Andean slopes from central Chile and the Patagonian Andes to Tierra del Fuego. The *minor* group is found in the northern Patagonian Andes, central and northern Chile, including possibly *G. bolivianus* from Bolivia. The other groups are also found at high altitudes. The *multifilis* group is known from only a single species taken at one locality in Ecuador. The *cilicinus* group extends from Ecuador to the central Andes of Argentina, the *brophyi* group from Venezuela to Tierra del Fuego, and the *cormonsi* group from Venezuela to northern Chile. The widest distribution is shown by the *wrighti* group that occurs from Mexico to Tierra del Fuego. The pupae of the *wrighti* group have highly variable gills, which could explain their ability to occupy different habitats.

Most of the species have a limited distribution. The exceptions are those from central Chile and the Patagonian Andes. These have a distributional range of about 2500 km from north to south. One reason could be the capability to compensate temperature with altitude or different seasons of the year. We saw this phenomenon for species from well-collected regions. Perhaps with more collections the same will be seen for species that are now known from restricted areas.

SYSTEMATICS

KEY TO SPECIES GROUPS

Adults

1. Without calcipala (figs. 2H, 8T). Subbasal tooth claw obsolescent (figs. 1J, K, 8U) and mandible and maxilla reduced or absent in females (figs. 1E, F, 8H–L); ventral plate enlarged in males (fig. 5K) .... *cortesi* group
   With calcipala, subbasal tooth claw well developed, mandible and maxilla with teeth well developed; ventral plate not enlarged in males 2
2. Subbasal tooth of claw hook-shaped in females (figs. 17M, 23P, 27J, K); aedeagal membrane with spinules (figs. 19A, B, G, 24P), ventral plate with a concavity distally in males (figs. 19A, E, 24N) 3
   Subbasal tooth of claw subtriangular or subrhomboidal; aedeagal membrane without spinules, and ventral plate without a concavity distally in males 4
3. Gonapophyses with distal border elongated (fig. 17N, O), spermatheca normal size, mandible with teeth only on inner side; spinules of aedeagus well developed, some of them sclerotized basally and fused like a shield (fig. 19A, B, G) ..... *igniculus* group
   Gonapophyses with distal border not elongate, only lobulate, spermatheca large, distinctly developed (figs. 23R, S, 27L); mandible with teeth on both sides (figs. 23C, D, 27C); spinules of aedeagus poorly developed (fig. 24P) ..... *minor* group
4. Sensorial vesicle of maxillary palp poorly developed (fig. 33D); gonapophyses with distal border lobulate; calcipala close longer than second tarsomere (fig. 33Q) .... *multifilis* group
   Sensorial vesicle well developed, gonapophyses with distal border straight; calcipala not attaining or surpassing the half of second tarsomere; with or without spinules on R_1, subbasal tooth claw subrhomboidal or subtriangular ..... *brophyi, cilicinus, cormonsi,* and *wrighti* groups

Pupae

1. Gill branches arborescent with over 100 terminal filaments 2
   Gill branches with not more than 18 terminal filaments, or branches with tubular or globose shape 4

TABLE 1
Index of Species of *Gigantodax* Cited in the Text, Figures, and Available Material from Various Life Stages

	F	M	Pupa	Larva	Figs.
abalosi	X	X	X	X	123–125
antarcticus	X	X	X	X	43–46
aquamarensis	X	X	X	X	145, 146
araucanius	X	X	X	–	23–25
arrarteorum	X	X	X	X	99–103
awa	X	X	X	–	64
basinflatus	X	X	X	X	89–91
bettyae	X	X	X	X	140–142
bolivianus	X	–	–	–	31
bonorinorum	–	–	–	–	–
brevis	X	X	X	X	115–117
brophyi group	–	–	–	–	37–80, 178C
brophyi	X	X	X	X	37–40
carmenae	–	X	X	X	14–16
cervicornis	X	X	X	X	147–150
chacabamba	–	–	X	X	12
chilensis	X	X	X	X	59–61, 178C
cilicinus group	–	–	–	–	81–109, 178E
cilicinus	–	X	X	X	106–108
clandestinus	X	X	X	X	104, 105, 178E
conviti	–	–	–	–	–
cormonsi group	–	–	–	–	110–137, 178D
cormonsi	X	X	X	X	126–128
corniculatus	X	X	X	X	151–153, 178F
cortesi group	–	–	–	–	1–13
cortesi	X	X	X	X	1–4
cypellus	X	X	X	X	174–176
destitutus	X	X	X	X	87, 88
dryadicaudicis	X	–	X	X	162–164
eremicus	–	–	X	X	26
femineus	X	X	X	X	49, 50
flabellus	X	–	X	–	62, 63
fulvescens	X	X	X	X	81–83
gracilis	X	X	X	X	110, 111
herreri	X	X	X	X	167–168
cf. *herreri*	–	–	X	–	169
horcotiani	X	X	X	X	138, 139
igniculus group	–	–	–	–	13–22, 178A
igniculus	X	X	X	X	17–22, 178A
impossibilis	X	X	X	X	170–173
incapucara	X	–	X	X	165, 166
incomitatus	–	X	X	–	93
jatunchuspi	X	X	X	X	5–7
kuscheli	X	–	–	X	55, 56
laevigatus	X	X	X	X	76–78
leonorum	X	X	X	X	122
near *leonorum*	–	–	–	–	–
luispenae	X	X	X	X	57, 58
marginalis	X	X	X	X	51–54
mariobordai	–	–	X	–	92
minor group	–	–	–	–	23–30, 178B
minor	X	X	X	X	27–30, 178B

TABLE 1—(*Continued*)

	F	M	Pupa	Larva	Figs.
misitu	X	X	X	X	112–114
multifilis group	—	—	—	—	33–36
multifilis	X	X	X	X	33–36
multituberculatus	X	X	X	X	73–74
nasutus	X	—	X	—	157, 158
nigrescens	—	—	—	—	—
ortizi	X	X	X	X	68–72
paramorum	X	X	X	X	65–67
patihuaycensis	—	X	X	—	75
pennipunctus	X	X	X	X	94–98
philippianus	—	—	—	—	—
praealtus	—	—	X	—	129
punapi	X	X	X	X	8–11
rufescens	X	X	X	X	159–161
rufidulus	X	X	X	X	41, 42
rufinotum	—	—	—	—	—
septenarius	X	X	X	X	143, 144
shannoni	X	X	X	X	84–86
siberianus	X	X	X	X	133–136
tarsatum	—	—	—	—	—
trifidus	X	X	X	X	47, 48
vargasi	—	—	—	—	—
vianamartinsi	—	—	—	—	—
vulcanius	X	X	X	X	130–132, 178D
wrighti group	—	—	—	—	138, 178F
wrighti	X	X	X	X	154–156
zumbahuae	—	—	X	—	79
wygodzinskyi	X	X	X	X	118–120
wygodzinskyi × *brevis*	—	—	X	—	121

2. Species with facial, labial, or frontal trichomes (figs. 4D, 10G, H); terminal filament branches starting beyond base of primary branches (figs. 6B, 10C) ..... *cortesi* group
   Species only with facial trichomes; terminal filamentous branches starting generally from secondary, tertiary, or more divided branches (figs. 20A–E, 35A, C) 3
3. Terminal spines thin and pointed (fig. 35K); abdominal tergite I with 3 + 3 or 4 + 4 hairy trichomes (fig. 35H) ..... *multifilis* group
   Terminal hooks stout (figs. 15G); abdominal tergite I with 5 + 5 or 7 + 7 trichomes (fig. 21B, C) ..... *igniculus* group
4. Gill filamentous branches not thicker basad and without tegumentary process (figs. 29A–E, 60A–E) 5
   Gills with tubular or subglobose branches, with cuticular processes; if they are filamentous they are thickened basally and generally 12th and 16th more elongated (figs. 10A–C, 127D, 155A–I) 6
5. 11–13 relatively flexuous gill branches (figs. 25A–C, 26A, B); terminal hook thin and elongated, pointed distally (figs. 25H, 26F), trichomes of frontoclypeus and thorax hooked distally (fig. 29G, H) . *minor* group
   18 relatively resistant (not flexuous) gill branches (figs. 39A–D, 60A–H); terminal spines stout (fig. 39H, I); trichomes of frontoclypeus and thorax not hooked ..... *brophyi* group
6. Gill branches with 17–18 tubular branches, generally with tegumentary processes (figs. 96E, 101B, C, E–H) 7
   Gill branches reduced in number, globose with cuticular processes or membranous (figs. 141A–E, 148A–D, 168A, B, N) ..... *wrighti* group
7. Branches independent (figs. 105A–D 107B, D) ..... *cilicinus* group
   Branches often fused making a shieldlike formation (figs. 116A, 131A–D, 135B, E, F) ..... *cormonsi* group

Larvae

1. Basal segment of antenna at most half as long as second (figs. 4F, 22C); second antennal segment as long as third (figs. 4F, 16G, H); median tooth of hypostomium longer than corner teeth, and imaginary line that goes from medium to fourth lateral not intersecting the others (figs. 4N, 16J, K, 22G); numerous mandibular serrations (figs. 4L, 16M, N, 22D) 2

   Second antennal segment not longer than first or third, median tooth of hypostomium not longer than corner teeth, if there is at higher level, a line crossing from median to fourth lateral teeth intersects the others; few mandibular serrations 3

2. Cephalic apotome widest near base (figs. 4D, 7B, 11B); recurrent struts well developed; second antennal segment 1.2–1.5 times longer than first (figs. 4F, 7D, 11C) ..... *cortesi* group

   Cephalic apotome widest near middle (fig. 16E); recurrent struts not well developed (fig. 22H); second antennal segment over 3 times longer than first (figs. 16G, H, 22C) ..... *igniculus* group

3. Third antennal segment longer than first and second together; second segment very short, less than one-third of basal (figs. 26H, 30D, E); anal scales reduced, not completing a ring ..... *minor* group

   Third antennal segment shorter than first and second together; basal segment about twice (or more) size of second segment; anal scales well developed, forming a ring 4

4. Anal gills with numerous lobules (more than three, fig. 36N;) mandible with reduced marginal serrations (fig. 36G–I) ..... *multifilis* group

   Anal gill with only three lobules; mandible with abundant marginal serrations ..... *brophyi, cilicinus, cormonsi,* and *wrighti* groups

KEY TO SPECIES

Adult Females

1. Species black; without calcipala (fig. 8T); claw with basal tooth small and without transversal sulci (figs. 1J, K, 8U); mandible and maxilla without or with very reduced teeth (figs. 1E, F, 8H–K) 2

   Species of different coloration, mostly yellowish to brownish; with calcipala; claw with basal tooth well developed and with transversal sulci (fig. 178A–F); mandible with 55 teeth; maxilla with more than 20 teeth 4

2. Wing length 5.0–6.0 mm; front relatively wide (figs. 8A–C); frontal angle about 130° .. 3

   Wing length about 4.3 mm; front relatively narrow (fig. 1A); frontal angle about 110° (N Chile, over 3000 m) ..... *cortesi*

3. Wing length 6.0 mm; ocellar triangle gradually elongated (fig. 5B) (N Chile) ..... *jatunchuspi*

   Wing length 5.0 mm; ocellar triangle wider than high (fig. 8E) (NW Argentina, Bolivia [La Paz], and N Chile) ..... *punapi*

4. Claw with subbasal tooth thin and acuminate distally as a hook (figs. 17M, 23P, 27J, K, 31G–I) 5

   Claw with subbasal tooth relatively wide distally, with subtriangular or subrhomboidal shape 8

5. Calcipala shorter than half of hind metatarsus length (fig. 17L); gonapophyses relatively elongated (fig. 17N, O) (Patagonian Andes) ..... *igniculus*

   Calcipala surpassing half of hind metatarsus length; gonapophyses not elongate (figs. 23R, 27L, 31K) 6

6. Species blackish, scutum, scutellum, metanotum, and legs dark brown to black; spinules or spiniform setae on R_1 beginning before the distal curvature of Sc (figs. 23I, J) (Patagonian Andes) ..... *araucanius*

   Species yellowish to reddish brown, with scutum, scutellum, and metanotum from orange to reddish brown; spinules on R_1 beginning after intersection of Sc and C or without spinules 7

7. Large species, wing length 7.0–7.4 mm; Sc with about 40 hairs (Bolivia, E of La Paz) ..... *bolivianus*

   Small species; wing length 2.6–3.4 mm. Sc with 11–20 hairs (Patagonian Andes and central Chile) ..... *minor*

8. Calcipala not attaining the center of hind metatarsus (figs. 43CC, 159G) 9

   Calcipala attaining or surpassing the center of hind metatarsus 15

9. Wing length 6.0 mm (Ecuador) ..... *clandestinus*

   Wing length 3.7–5.4 mm 10

10. Scutum, scutellum, metanotum, legs, and abdomen yellowish to light orange; claw with a basal tooth subtriangular, very elongate (fig. 159D) (Patagonian Andes and central Chile) ..... *rufescens*

    Scutum, scutellum, metanotum, legs, and abdomen from yellowish brown to dark brown; claw with a basal tooth variable, but shorter than in *rufescens* 11

11. Wing length about 4.9–5.4 mm, with spinules on R_1 12
Wing length between 3.7 and 5.0 mm, without spinules on R_1; if spinules present, wing length not more than 4.7 mm 13
12. Scutum, scutellum, and metanotum dark brown; antenna brown; mandible with 30–34 teeth (Peru) ..... *herreri*
Scutum, scutellum, and metanotum dark purple with pronotal sclerites yellowish; antenna orange; mandible with 21 teeth (fig. 99B) (E Andes of Peru) ..... *arrarteorum*
13. R_1 without spinules; scutum and scutellum orange to light brown or reddish brown (Patagonian Andes) .... *antarcticus* + *trifidus* + in part *brophyi* + in part *rufidulus*
R_1 with spinules; scutum and scutellum light reddish brown 14
14. Scutum with central area darker; frontal angle 50°; ratio length/width hind basitarsus = 6.9–7.6 (Peru) ..... in part *cormonsi*
Scutum with homogeneous coloration, without central area darker; frontal angle 55–60°; ratio length/width of hind basitarsus = 9.5 (NW Argentina) ..... *horcotiani*
15. Calcipala length half that of hind metatarsus (figs. 49I, 174B) 16
Calcipala longer than half of hind metatarsal length (figs. 81H, 157N, etc.) 20
16. Wing length 5.0–5.6 mm; claw with basal tooth subtriangular, elongate (fig. 174M) (Ecuador) ..... *cypellus*
Wing length 3.5–4.7 mm; claw with basal tooth subtrapezoidal (fig. 41I) or subtriangular (fig. 94I) 17
17. Wing length 3.5–4.3 mm; scutum bronze-brown to yellowish brown or light reddish-brown with center dark brown 18
Wing length 4.3–4.7 mm; scutum light brown (Peru, Cuzco) ..... *pennipunctus*
18. Without spinules on R_1; scutum and metanotum bronze-brown or homogeneous light reddish-brown; legs light brown (Patagonian Andes) .. *femineus* + in part *rufidulus*
With spinules on R_1; scutum orange or light reddish brown with center area dark brown 19
19. Scutum orange; cercus extraordinarily compressed dorsoventrally, paraproct apex with a group of long hairs (fig. 162P) ....in part *dryadicaudicis*
Scutum light reddish-brown, with center area dark brown; cercus and paraproct normal (Peru) . in part *abalosi* + in part *cormonsi* (Ecuador) ... in part *leonorum* (Colombia) ... in part *siberianus*
20. Mouth parts very elongate (fig. 157A, E, F); scutum very light reddish-brown, scutellum yellow, mandible and maxilla with 50 teeth (Colombia) ..... *nasutus*
Mouth parts normal; scutum and scutellum and number of teeth of mandible and maxilla variable 21
21. Scutum yellow to brownish orange 22
Scutum yellowish brown, dark purple, to dark brown 28
22. Abdomen piceous to dark brown 23
Abdomen yellow to light brown 27
23. Wing length 3.3–3.5 mm; scutum orange or yellow; legs light brown to golden 24
Wing length 3.9–4.5 mm; scutum orange to reddish-brown; legs yellow to light orange 25
24. Abdominal tergites I–III golden brown, IV–IX dark brown; frontal angle 45°; cercus and paraproct normal (Colombia and W Venezuela) .....*destitutus*
Abdominal tergite I yellowish, remaining dark gray; frontal angle 75°; cercus and paraproct compressed dorsoventrally, paraproct apically with a group of long, strong setae (fig. 162P) (central Chile) .... *dryadicaudicis*
25. Wing length 4.3–4.5 mm; scutum reddish-orange (Venezuela) .... in part *impossibilis*
Wing length 3.9–4.2 mm; scutum brownish-orange or orange to reddish-brown ... 26
26. Maxilla with 25 teeth; ratio length/width of basal article of maxillary palp = 0.38–0.42; ratio length/width of hind basitarsus = 7.2–7.8 (Ecuador, Colombia, Venezuela) .... *cervicornis*
Maxilla with 35 teeth; ratio length/width of basal article of maxillary palp = 0.45–0.48; ratio length/width of hind basitarsus = 6.6 (Colombia) ..... *paramorum*
27. Wing length 3.5–3.7 mm; abdominal tergites brownish; maxilla with 25 teeth; calcipala about as wide as long (fig. 81H) (Patagonian Andes) ..... *fulvescens*
Wing length 4.2–4.8 mm; abdominal tergites yellowish; maxilla with 34 teeth; calcipala longer than wide (fig. 84R) (Patagonian Andes and central Chile) ..... *shannoni*
28. Wing length over 4.5 mm 29
Wing length less than 4.4 mm 37
29. Mandible with 30–35 teeth (Colombia) .... in part *wygodzinskyi*
Mandible with 16–29 teeth 30
30. Antenna black; mandible with 27–29 teeth (Ecuador) ..... *vulcanius*
Antenna dark brown; mandible with 16–26 teeth 31
31. Frontal angle 30–40° 32
Frontal angle about 50° 33

32. Wing length 4.3–4.9 mm; frontal angle 30–35° (Colombia) ..... in part *brevis*
Wing length 5.0–5.2 mm; frontal angle 35–40° (Ecuador, Colombia) ..... *misitu*
33. Mandible with 16–20 teeth (Ecuador) ..... *gracilis*
Mandible with 22–25 teeth 34
34. Calcipala about two-thirds the length of hind metatarsus; calcipala longer than wide 35
Calcipala about four-fifths the length of hind metatarsus; calcipala shorter than or as long as wide 36
35. Wing length 4.5–5.0 mm; ratio length/width hind basitarsus = 6.2–6.3; scutum with central portion darkest (Ecuador) . *leonorum*
Wing length 4.3–4.5 mm; ratio length/width hind basitarsus = 4.2. Scutum with homogeneous pigmentation, without dark central portion (Patagonian Andes) ..... in part *rufidulus*
36. Calcipala shorter than wide (fig. 151H); maxilla with 26 teeth (Venezuela) ..... *corniculatus*
Calcipala as long as wide (fig. 126I); maxilla with 23 teeth (E Andes of Peru) ..... in part *cormonsi*
37. Claw with subbasal tooth very small (fig. 154P); mandible with 18–21 teeth, maxilla with 16–19 teeth (Mexico) ..... *wrighti*
Claw with subbasal tooth well developed; mandible and maxilla with 20–35 teeth .. 38
38. Spermatheca with sclerotized neck base (fig. 89Q); claw with basal teeth subtriangular and elongated (fig. 89G–I); ratio length/width of hind basitarsus = 8.4–8.8 (Colombia, Ecuador) ..... *basinflatus*
Spermatheca with base of neck not sclerotized; claw with basal tooth subtriangular or subrhomboidal; ratio length/width of hind basitarsus = 6.6–8.2 39
39. Scutum light reddish-brown, with central portion darkest; scutellum yellowish-brown, metanotum dark brown; legs pale yellow; abdominal terga piceous to brass colored 40
Scutum, scutellum, metanotum, legs, and abdominal terga with different combination of colors 44
40. Frontal angle 30–35° 41
Frontal angle 45–50° 42
41. Ratio length/width of hind basitarsus = 7.2–7.9; mandible and maxilla with 23–26 and 21–23 teeth, respectively; Sc with 29–32 hairs (Colombia) ..... in part *brevis*
Ratio length/width of hind basitarsus = 6.6–6.7; mandible and maxilla with 30 and 28–30 teeth, respectively; Sc with 33–38 hairs (Colombia) ..... *wygodzinskyi*
42. Mandible with 30–35 teeth and maxilla with 28 teeth (Colombia) .. in part *siberianus*
Mandible with 22–25 teeth and maxilla with 23 teeth 43
43. Wing length 3.7–4.1 mm; ratio length/width of hind basitarsus = 7.8 (W Andes of Peru) ..... in part *abalosi*
Wing length 4.3–4.7 mm; ratio length/width of hind basitarsus = 6.9–7.6 (E Andes of Peru) ..... in part *cormonsi*
44. Wing length over 4.3 mm 45
Wing less than 4.2 mm 47
45. Frontal angle 55–60°; mandible with 21–33 teeth (W Venezuela) ..... in part *bettyae*
Frontal angle 30–50°; mandible with 24–30 teeth 46
46. Wing length 4.3–4.4 mm; frontal angle 45°; mandible with 30 teeth (Venezuela) ..... in part *impossibilis*
Wing length 4.6–4.8 mm; frontal angle 50°; mandible with 24 teeth (W Venezuela) .. *corniculatus*
47. Scutum yellowish to brown 48
Scutum reddish-brown or dark purple .. 49
48. Scutum under certain illuminations shows median longitudinal stripe; metanotum dark brown; calcipala three-quarters of length of hind metatarsus (fig. 59W, X) (Patagonian Andes and central Chile) ..... *chilensis*
Scutum without median longitudinal stripe; calcipala two-thirds of length of hind metatarsus (figs. 51N–P) (Patagonian Andes and central Chile) ..... *marginalis*
Islas de Juan Fernandez . . . *kuscheli*
49. Wing length under 3.6 mm 50
Wing length over 3.7 mm 53
50. Scutum and metanotum dark purple; scutellum light brown (Ecuador) ... *laevigatus*
Scutum reddish-brown; scutellum and metanotum variable 51
51. Scutellum from stramineous to light brown; metanotum light reddish brown (Colombia) ..... *septenarius*
Scutellum and metanotum dull reddish-brown 52
52. Mandibles with 22 teeth and maxillae with 22–24 teeth (Guatemala) .. *aquamarensis*
Mandibles with 24 teeth and maxilla with 35 teeth (central Chile) ..... *luispenai* + in part *marginalis*
53. Frontal angle 55–60° (W Venezuela) ..... in part *bettyae*
Frontal angle 40–45° 54
54. Scutum dark purple, maxilla with 36–38 teeth (Venezuela) ..... *ortizi*

Scutum from light to dark reddish-brown; maxilla with 25–27 teeth 55

55. Scutum light reddish-brown 56
Scutum dark reddish-brown (Ecuador) .... *multifilis*

56. Ratio length/width of hind basitarsus = 8.2; Sc with 19 hairs (Peru, Machupicchu) ... . *incapucara*
Ratio length/width of hind basitarsus = 6.5–6.9; Sc with 26–28 hairs (Colombia and Ecuador) ..... *multituberculatum*

Not included in the key because of inadequate information are *awa, flabellus,* and *praealtus.* Unknown as females are *chacabamba, carmenae, cilicinus, eremicus, incomitatus,* and *zumbahuae.* We were unable to see specimens of *conviti, mariobordai,* and *patyhuaicensis.*

Adult Males

1. Dichoptic (fig. 49W); scutum, scutellum, and metanotum reddish-brown; calcipala slightly shorter than half of second hind tarsomere (Patagonian Andes) ... *femineus*
Holoptic; scutum, scutellum, and metanotum of variable coloration; calcipala about half the length of second tarsomere 2

2. Without calcipala (fig. 2H); body blackish, ventral plate enlarged (figs. 2L, O, 5K); with small interocular space (fig. 2A) 3
With calcipala; body generally brown to yellow; eyes without interocular space ... 5

3. Wing length 3.7–3.9 mm (N Chile) .... *cortesi*
Wing length over 4.0 mm 4

4. Wing length about 4.5 mm (NW Argentina, N Chile, and Bolivia) (La Paz) ... *punapi*
Wing length about 5.5 mm (N Chile) .... *jatunchuspi*

5. Wing length 5.0–6.2 mm 6
Wing length less than 4.9 mm 9

6. Ratio of length distimere/basimere 1:1 (fig. 99T) 7
Ratio of length distimere/basimere about 2:3 8

7. Wing length about 5.0 mm; distimere with 3 hooks (fig. 99T); ratio length/width of hind basitarsus = 5.8 (W Andes of Peru) .... *arrarteorum*
Wing length about 6.2 mm; distimere with 2 hooks (fig. 104J); ratio length/width of hind basitarsus = 6.5 (Ecuador) . *clandestinus*

8. Wing length 5.5 mm; calcipala wider than high; calcipala shorter than half length of second hind basitarsus (fig. 106I); ratio length/width of hind basitarsus = 6.6–7.1 (central Andes of Argentina [San Juan]) ..... *cilicinus*
Wing length 4.8–5.1 mm; calcipala shorter than wide, calcipala longer than half length of second hind tarsomere (fig. 174O); ratio length/width hind basitarsus = 5.8–6.0 (Ecuador) ..... *cypellus*

9. Antenna, scutum, and metanotum black; R_1 with spinules or spiniform setae beginning below level where Sc ends (fig. 24H) (Patagonian Andes) ..... *araucanius*
Antenna, scutum, and metanotum from yellow or orange to dark brown; R_1 generally with spinules beginning above level of Sc end, or without spinules 10

10. Scutum yellow, orange, or reddish-orange 11
Scutum dark reddish, reddish-brown, grayish-brown, or dark brown 26

11. Calcipala shorter than or equal to half length of second tarsomere 12
Calcipala longer than half length of second tarsomere 15

12. Scutum from yellowish-brown to rust-colored with white median longitudinal stripe; calcipala reaching middle of second tarsomere (fig. 95I) (Peru: Cuzco) ..... *pennipunctus*
Scutum yellow to orange-reddish, without median stripe; calcipala shorter than half of second tarsomere 13

13. Wing length 3.3 mm; aedeagal membrane with abundant and stout spinules (fig. 19A, B, G); ratio length/width hind basitarsus = 4.7 (Patagonian Andes) ..... *igniculus*
Wing length 4.2–4.7 mm; aedeagal membrane only with small spicules; ratio length/width of hind basitarsus = 6.0–7.8 14

14. Distimere about one-half length of basimere; without spinules on R_1; ratio length/width of hind basitarsus = 6.0; legs light brown (Patagonian Andes) .....in part *brophyi*
Distimere over two-thirds the length of basimere; with spinules on R_1; ratio length/width of hind basitarsus = 7.0–7.8; legs pale yellow (Patagonian Andes and central Chile) ..... *rufescens*

15. Wing length over 4.0 mm 16
Wing length less than 3.9 mm 20

16. Metanotum yellow; distimere about three-quarters of basimere length (fig. 84C); Sc with 27–29 hairs (Patagonian Andes and central Chile) ..... *shannoni*
Metanotum yellowish-brown to reddish-brown; distimere about two-thirds basimere length; Sc with 16–23 hairs 17

17. Scutum bright reddish-orange; ratio length/width of hind basitarsus = 6.5–7.0; Sc with 14–16 hairs (Venezuela) ... *corniculatus*
Scutum yellow orange; ratio length/width of

hind basitarsus = 6.8–7.8; Sc with 5–23 hairs 18

18. Metanotum reddish-orange; calcipala shorter than wide (Venezuela) ..... *impossibilis*
Metanotum light brown to brownish-orange; calcipala longer than or as long as wide 19

19. Calcipala as long as wide (fig. 64K); Sc with 23 hairs (Peru, Cuzco) ..... *awa*
Calcipala longer than wide (fig. 147I); Sc with 16–18 hairs (Ecuador, Colombia, and Venezuela) ..... *cervicornis*

20. Species without spinules on R_1; metanotum dark brown (Patagonian Andes and central Chile) ..... *minor*
Species with spinules on R_1; metanotum from yellowish to light brown 21

21. Wing length 2.9–3.3 mm 22
Wing length 3.5–4.1 mm 23

22. Calcipala about three-quarters length of hind basitarsus, wing length 3.2–3.3 mm (Patagonian Andes and central Chile) *chilensis*
Calcipala about four-fifths length of hind basitarsus (fig. 87N); wing length 2.9–3.1 mm (Colombia and W Venezuela) .... *destitutus*

23. Ratio length/width of hind basitarsus = 5.0–5.5 mm (Patagonian Andes and central Chile) ..... *fulvescens*
Ratio length/width of hind basitarsus = 5.9–7.8 mm 24

24. Distimere with two large and one small apical spines (fig. 65M) (Colombia) .... *paramorum*
Distimere with only two large apical spines 25

25. Metanotum brownish-orange to light brown; wing length 3.9–4.1 mm (Ecuador, Colombia, and Venezuela) .(in part) *cervicornis*
Metanotum bright reddish-brown to pale reddish-brown. Wing length 3.6–3.9 (Ecuador and Colombia) .... *multituberculatus* + *septenarius*

26. R_1 without spinules 27
R_1 with spinules 28

27. Scutum, scutellum, and pleurae from light grayish-brown to blackish-gray; ratio length/width of hind basitarsus = 4.2–5.5 (Patagonian Andes) .... *antarcticus* + *trifidus*
Scutum light reddish-brown to orange, scutellum and pleurae pale brown; ratio length/width of hind basitarsus = 6.0–6.5 (Patagonian Andes) ..... (in part) *brophyi*

28. Ratio length/width of hind basitarsus = 7.3–7.7 29
Ratio length/width of hind basitarsus = 5.0–7.0 31

29. Distimere about one-third length of basimere (fig. 52S) (Patagonian Andes and central Chile) ..... (in part) *marginalis*
Distimere between one-half and two-thirds length of basimere 30

30. Scutum dark reddish-brown; fore basitarsus 9.5–10.7 times longer than wide (Peru and Bolivia) ... *patyhuaycensis* + *incapucara*
Scutum dark brown; fore basitarsus 12 times longer than wide (Colombia and Ecuador) ..... *basinflatus*

31. Metanotum yellowish to light reddish-brown 32
Metanotum dark reddish-brown, grayish-brown, dark brown, or blackish 43

32. Calcipala shorter than, or equal to, half the length of second tarsomere 33
Calcipala longer than half the length of second tarsomere 35

33. Ratio length/width of hind basitarsus = 6.6–7.0 (eastern Andes of Peru) ... *cormonsi*
Ratio length/width of hind basitarsus = 5.0–6.0 34

34. Ratio length/width of hind basitarsus = 5.0–5.5 (Patagonian Andes) ..... *rufidulus*
Ratio length/width of hind basitarsus = 5.9–6.0 (Ecuador) ..... *leonorum*

35. Wing length 3.2–3.8 mm 36
Wing length 3.9–4.6 mm 41

36. Ratio length/width of hind basitarsus = 5.0–6.2 37
Ratio length/width of hind basitarsus = 6.3–6.8 40

37. Distimere with two big and one small spine (fig. 65M) (Colombia) .... (in part) *paramorum*
Distimere with only two big spines 38

38. Scutum yellowish-brown; wing membrane infuscate (Patagonian Andes and central Chile) ..... *chilensis*
Scutum reddish-brown; wing membrane hyaline 39

39. Scutum dark chestnut brown; antenna grayish brown (Venezuela and Colombia) .. *ortizi*
Scutum brownish-orange; antennae light brown (Colombia) ..... *septenarius*

40. Antenna light brown; calcipala shorter than wide (fig. 140L); Sc with 15–17 hairs (W of Venezuela) ..... *bettyae*
Antenna dark brown; calcipala longer than wide (fig. 154S); Sc with 14 hairs (Mexico) ..... *wrighti*

41. Distimere with two or three spines; ratio length/width of hind basitarsus = 5.4–5.9 (Colombia) ..... *brevis*
Distimere with two spines; ratio length/width of hind basitarsus = 6.3–6.9 42

42. Antenna black (Ecuador) ..... *vulcanius*
Antenna dark brown (Ecuador) .... *gracilis*
43. Wing length over 4.0 mm 44
Wing length less than 3.9 mm 50
44. Ratio length distimere/basimere about one (Peru) ..... *herreri*
Ratio length distimere/basimere about one-half to three-quarters 45
45. Antenna blackish; ratio length/width of hind basitarsus = 6.9 (Ecuador) ..... (in part) *vulcanius*
Antenna brownish; ratio length/width of hind basitarsus = 5.4–6.8 46
46. Calcipala shorter than half the length of second tarsomere (fig. 38K); distimere about one-half the length of basimere (fig. 38L, M) (Patagonian Andes) ..... *brophyi* + (in part) *rufidulus* + (in part) *abalosi* (Peru)
Calcipala longer than half the length of second tarsomere; distimere about two-thirds to three-quarters the length of basimere . 47
47. Distimere about three-quarters the length of basimere (fig. 138R) (NW Argentina) .... *horcotiani*
Distimere about two-thirds the length of basimere 48
48. Scutum dark chestnut brown to light reddish-brown; legs light brown to pale yellow, base and apex of femora and tibia darkened (Ecuador) ..... *cypellus* (Patagonian Andes) ... (in part) *rufidulus*
Scutum dark brown; legs yellowish 49
49. Sc with 20 hairs; wing 4.1–4.2 mm (Colombia) ..... *siberianum*
Sc with 10–18 hairs; wing 4.6–4.8 mm (Ecuador, Colombia) ..... *misitu*
50. Calcipala about one-third the length of second tarsomere (fig. 14F); aedeagus with stout spines (Patagonian Andes) ... *carmenae*
Calcipala about one-half length of second tarsomere; aedeagus without stout spines 51
51. Ratio length/width of hind basitarsus = 7.0; scutum bright reddish orange (Ecuador, Colombia) ..... *multituberculatus*
Ratio length/width of hind basitarsus = 5.4–6.9; scutum reddish-brown to dark brown 52
52. Distimere about one-third length of basimere (Patagonian Andes and central Chile) ... . *marginalis* (Peru) (in part) ... *abalosi*
Distimere one-half to two-thirds length of basimere 53
53. Distimere about one-half length of basimere (fig. 145L) (Guatemala) ... *aquamarensis* (central Chile) ... *luispenai*
Distimere about two-thirds length of basimere 54
54. Ratio length/width of hind basitarsus = 6.3–6.6 (Mexico) ..... (in part) *wrighti*
Ratio length/width of hind basitarsus = 5.4–6.3 55
55. Ratio length/width of hind basitarsus = 5.4–5.9 (Ecuador) ..... *laevigatus* (Colombia) ... *wygodzinskyi*
Ratio length/width of hind basitarsus = 6.3 (Guatemala) ..... (in part) *aquamarensis*

Not included because of inadequate information are *flabellus, incomitatus,* and *multifilis.* We did not have material for *conviti* and *viannamartinsi.* The following are unknown: *bolivianus, chacabamba, dryadicaudicis, eremicus, kuscheli, mariobordai, nasutus, praealtus,* and *zumbahuae.*

Pupae

1. Gills each consisting of a pedunculate, spherical structure covered with very numerous respiratory filaments (fig. 15A, B) (Patagonian Andes) ..... *carmenae*
Gills different 2
2. Gills each in shape of a large funnel, its sides with a circle of about 18 respiratory filaments (fig. 175A–D) (Ecuador) . *cypellus*
Gills different 3
3. Gills each with three or four tubular branches, one of which is transformed into a large, subglobular structure 4
Gills not so 5
4. Gills each with three tubular branches in addition to a spherical one, the latter generally glabrous, its respiratory filaments caducous (fig. 172B–D, G–I) (Venezuela) .... *impossibilis*
Gills each with two tubular branches in addition to subglobular structure, the latter with a crown of non-caducous respiratory filaments (fig. 168A, B, N) (Bolivia and Peru) ..... *herreri*
5. Gills with more than 18 respiratory filaments 6
Gills each with from 4 to 18 free or partially fused branches; respiratory filaments, when present, not more than 18 11
6. Gills simple, each consisting of a bundle of about 55 filamentous branches, originating from simple dichotomous divisions of trunk and main branches (fig. 12A–D) (Peru) .. .. *chacabamba*
Gills arborescent, each with more than 100 branches and respiratory filaments 7

7. Main branches of gills directed forward, distinctly longer than thorax (figs. 6B–D, 10A, B) 8
Main branches of gill strongly divergent, much shorter than thorax (figs. 20A–E, 35A–C) 10
8. Gills each with five large primary branches; no conspicuous group of basal respiratory filaments (fig. 3B); sternite VIII with four peculiarly twisted setae (fig. 4B); frontal trichomes not developed (fig. 3D, E) (N Chile) ..... *cortesi*
Gills each with four large primary branches and with conspicuous group of basal respiratory filaments (figs. 6B–D, 10A–F); sternite VIII without setae mentioned; frontal trichomes rarely absent 9
9. Maximum length of gills 4 mm; body length of pupa 5.0–6.5 mm; cephalopterothecal length 3.2–3.8 mm; small perpendicular primary branches at base of gills well developed (fig. 10C); frontal trichomes approximately of same size as facial and labial trichomes (fig. 10H) (NW Argentina, Bolivia, N Chile) ..... *punapi*
Length of gills 5.5–6.5 mm; body length of pupa 7.5–8.0 mm; cephalopterothecal length 4.7–4.8 mm; small primary branches at base of gills obsolescent (fig. 6B) (N Chile) ..... *jatunchuspi*
10. Platelets of head and thorax conspicuously verrucose (fig. 35F); platelets of frontoclypeus very numerous, uniformly distributed except on glabrous spots (Ecuador) ..... *multifilis*
Platelets of head and thorax smooth; platelets of frontoclypeus not numerous, irregularly scattered (Patagonian Andes) .. *igniculus*
11. Gills consisting each of two medium-size and one very small dorsal and one medium-size ventral tubular branch, in addition to two anterolateral, very large, dorsoventrally flattened, tongue-shaped branches (fig. 166A, B) (Peru) ..... *incapucara*
Gills different 12
12. Gills consisting of 18 branches, some or all of which are fused into one, two, or three shieldlike structures 13
Number of gill branches varied, but gills not fused into shieldlike structures 20
13. Second to eighth dorsal gill branches fused into one shieldlike structure, 1st and 9th to 18th branches free 14
All branches fused, at least for most of their length, forming two or three shieldlike structures 15
14. 11th branch broadly rounded apically; 12th and 16th branches not over twice as long, with distinct elongate hairlike cuticular projections occurring all the way to base of respiratory filament (fig. 116A–D, F) (Colombia) ..... *brevis*
11th branch pointed apically in most specimens, 12th and 16th branches more than twice as long, and with short setalike cuticular projections restricted to base of branches (fig. 120A, B) (Colombia) ..... *wygodzinskyi*
15. Fused gill branches forming three shields, with none of the branches projecting beyond outlines of shields (fig. 135B, E, F) (Colombia) ..... *siberianus*
Some of gill branches projecting conspicuously beyond outlines of shields formed by branches 16
16. 1st to 14th gill branches forming dorsal, and 15th to 18th branches forming ventral shield (fig. 131A–D) (Ecuador) ..... *vulcanius*
Gill branches forming three shieldlike structures: a dorsal one from first to eighth branches, a lateral one including six and a ventral one consisting of four branches (figs. 122A, B, 124A–E, 127D, F, 129C, E) .. 17
17. Projecting gill branches with minute setalike cuticular processes 18
Projecting gill branches with tuberclelike cuticular processes 19
18. Facial trichomes and trichomes of dorsum of thorax short, spinelike (fig. 122C, E) (Ecuador) ..... *leonorum*
Facial trichomes and trichomes of dorsum of thorax long, hairlike (fig. 124G, K) (Peru) ..... *abalosi*
19. Individual components of dorsal shield formed by gill branches projecting much beyond margin of shield, their apical portions elongate, pointed (fig. 129C, E); thoracic platelets faint, not arranged in distinct pattern (Chile) ..... *praealtus*
Individual components of dorsal shield projecting little if any beyond margin of shield, their apical portions angular or broadly rounded (fig. 127A, B, D, F); thoracic platelets distinct, arranged in rosettelike pattern (fig. 127I) (Peru) ..... *cormonsi*
20. Gills consisting each of two dark, tree-trunklike, forwardly directed, subcylindrical, apically truncate branches of large diameter, and of six tubular, membranous, subvertical branches of smaller diameter (fig. 163A–D); abdomen with terminal spines very short (figs. 164L); abdominal tergite VIII with 2 + 2 unusually stout setae (fig. 164G) (S Chile) ..... *dryadicaudicis*
Gills and abdomen different 21
21. Gills compact, stout, consisting of 16–18 short

branches, with base wide and for most of their length, apex rather abruptly pointed and with long terminal respiratory filament; branches completely covered with numerous long hairlike cuticular processes (figs. 101B, C, 107C, D, 105L); main body of gills perpendicular to longitudinal axis of body of pupa; both gills combined somewhat starlike in appearance in frontal view (figs. 100, 101B, 107B) 22

Gills different 24

22. Abdominal sternite V with 3 + 3, sternal plates VI each with three and sternal plates VII each with two hooks; gills with branches of subequal size, general shape of gill regular; in most specimens, second to sixth secondary branches arising from common trunk, seventh and eighth arising together from short primary trunk; total number of secondary branches 18 23

Abdominal sternite V with 2 + 2, sternal plates VI each with two and sternal plates VII each with one hook (fig. 106N); gills with secondary branches of extremely varied sizes, general shape of gill highly irregular (figs. 106O–Q, 107B, D); in most specimens, second to fifth secondary branches arising from common trunk, sixth and seventh very short, arising together from elongate primary branch; total number of secondary branches 16–17, very rarely 18 (central Andes of Argentina: San Juan) .... *cilicinus*

23. Gill branches comparatively stout, more abruptly narrowed apically (fig. 105A–D, L) (Ecuador) ..... *clandestinus*

Gill branches more slender, more gradually narrowed toward apex (fig. 101B, C, E–H) (Peru) ..... *arrarteorum*

24. Gill consisting each of 18 branches arranged in a radiating pattern forming a semioval structure perpendicular to longitudinal axis of body of pupa; most branches comparatively short and entirely covered with spinelike cuticular processes; two branches projecting much beyond level of apex of remaining, beset for most of their length with small tuberclelike cuticular projections; respiratory filaments near base of branches (fig. 113A–G) (Colombia and Ecuador) ..... *misitu*

Gills different 25

25. Gills much shorter than cephalopterothecal length, their branches rigid, short, strongly acuminating toward apex (figs. 92A, 96A, B) 26

Gills in most species as long as, or longer than, cephalopterothecal length; structure of gill branches not as above 28

26. Gills tapered apically, with caducous respiratory filaments, their cuticula conspicuously wrinkled 27

Gills acuminated but not tapered without caducous respiratory filaments, their cuticula smooth, surface uniformly dotted; gills with 17 branches (fig. 92B, C, F, H) .... *mariobordai*

27. Gills with 18 branches, their apical portion with short but distinct cuticular processes (fig. 96C–E, I) (Peru) ..... *pennipunctus*

Gills with at most 14 branches; cuticular process absent (fig. 146F, L, Q, T) (Guatemala) ..... *aquamarensis*

28. Most or all gill branches tubular, rounded, or pointed apically, their distal portion not drawn out into elongate narrow structure 29

All gill branches filiform, or at least long and slender and with their apical portion drawn out into elongate, narrow structure ... 37

29. Thoracic gills with seven branches, their shape lanceolate, narrowed on basal half or third of their length (Venezuela) ..... *conviti*

Thoracic gills with eight or more branches or projections corresponding to branches . 30

30. Gill branches of somewhat irregular shape, dark, conspicuously wrinkled, in no case with cuticular processes 31

Gill branches of very regular shape, light colored, not conspicuously wrinkled, with or without cuticular processes 33

31. Gills shorter than cephalopterothecal length, with not more than nine branches, these generally rounded apically, some conspicuously swollen distally (fig. 155A–I) (Mexico and Guatemala) ..... *wrighti*

Gills longer then cephalopterothecal length, with more than nine branches, most pointed apically and none swollen distally . 32

32. Facial trichomes spinelike (fig. 155F); each gill with four long, slender branches in addition to short ones; all branches fully developed even though some very short (fig. 152A, B, G, H) (Venezuela) . *corniculatus*

Facial trichomes hairlike (fig. 149A); each gill with one long and slender branch in addition to short ones; some of the branches reduced to swellings bearing a respiratory filament (fig. 148A–D) (Venezuela and Ecuador) ..... *cervicornis*

33. Gill branches short and wide, subcylindrical, broadly rounded at apex, without cuticular processes 34

Gill branches comparatively long and slender, somewhat pointed at apex, with or without distinct setalike cuticular processes ... 35

34. Gills each with four tubular branches (fig.

160A, D, E); anterosublateral setae of abdominal tergites III and IV absent (Patagonian Andes) ..... *rufescens*

Gills each with five branches (fig. 158A, B, D, F); anterosublateral setae of tergites III and IV present (fig. 158I) (Colombia) . *nasutus*

35. Gills with 12–14 branches, the dorsal ones not overlying body of pupa (fig. 139A–C, I) (NW Argentina) ..... *horcotiani*

Gills with fewer than 10 branches, the dorsal ones overlaying body of pupa 36

36. Gills each with nine branches, all except first dorsal one arising in pairs from four short trunks (fig. 141A–C, E) (Venezuela) ..... *bettyae*

Gills each with seven branches, arising individually from one basal trunk, except second and third which share common trunk (fig. 144A, B, D, F) (Colombia) ..... *septenarius*

37. Gill branches in fanlike arrangement, beset on basal portion with spinelike cuticular processes (fig. 111A–C, I); frontoclypeus without distinct platelets (Ecuador) ..... *gracilis*

Gill branches in fanlike arrangement or not, but not with spinelike cuticular processes; frontoclypeus in most but not all species with distinct platelets 38

38. Secondary gill branches numbering 17, arising in groups of four to five from conspicuously swollen primary branches (figs. 90A–E, 91L, O, P) (Colombia and Ecuador) ..... *basinflatus*

Secondary gill branches not numbering 17 and not arising in groups of four to five from conspicuously swollen primary branches 39

39. Gills consisting of from 10 to 13 branches 40

Gills consisting of 18 (very rarely 16) branches 43

40. Main body of gills situated in a plane roughly perpendicular to longitudinal axis of body of pupa, with apical portion of branches directed slightly caudad; branches of gills widely diverging, not filamentous, the second and fourth branches—counted from below—rounded apically, the remaining pointed; basal trunk of gills very short, not longer than wide (fig. 93A, B, I) (Venezuela) ..... *incomitatus*

Gills directed forward; branches subparallel, filiform, forming a tight bundle; basal trunk of gills elongate, several times as long as wide; some trichomes of head and thorax hooked apically 41

41. Gills each with 13 branches (fig. 26A, B) .. *eremicus*

Gills each with 11 branches (figs. 25A–C, 29A–E) 42

42. Gills open, not pedunculate; primary branches emerging very close to body, without stem (arising from a short basal trunk) (fig. 25A–C); head and dorsal surface with very few platelets (fig. 25D–F) (Patagonian Andes) ..... *araucanius*

Gills arranged in bundle and pedunculate; primary branches emerging from a relatively long stem (fig. 29A–E); head and thorax with numerous platelets (fig. 29F–H) (Patagonian Andes and central Chile) ... *minor*

43. Gills with branches directed forward, forming compact bundle in a fan or scoop-shaped group; when branches somewhat diverging at base, then not divided into distinct ventral and dorsal group (species mostly from the Andes north of Bolivia, except *chilensis* (Patagonian Andes and central Chile) . 44

Gills with branches not forming compact bundle; gill branches conspicuously divergent at least proximally, in many instances their basal portion more or less perpendicular to longitudinal axis of body of pupa in many cases, branches divided into ventral and dorsal groups (species mostly form the Chilean–Patagonian area, except *destitutum* [Colombia, Venezuela] and *paramorum* [Colombia]) 51

44. Thorax completely glabrous, or at least with platelets absent from large area around insertion of dorsolateral trichomes 45

Thorax with numerous platelets distributed over entire dorsal surface 46

45. Platelets of thorax completely absent; secondary and tertiary branchings remote from base of gills (fig. 77C–E) (Ecuador) ..... *laevigatus*

Platelets numerous along dorsal suture and scattered on lateroventral area of thorax (fig. 75I); secondary and tertiary branchings of gills extremely close to their base (fig. 75J) (Peru) ..... *patihuaycensis*

46. Gill branches either subparallel for almost their entire length and forming a more or less tight bundle, or distinctly diverging on basal portion and forming a fan or scoop-shaped structure with the concavities formed by the gills face to face; setae of first abdominal tergite longer than those of second (Andean region of N Bolivia) 47

Each gill with branches strongly diverging basally and forming a loose calyx-like structure (fig. 60A–E); setae of first abdominal tergite shorter than those of second (Patagonian Andes and central Chile) . *chilensis*

47. Gill branches subparallel for almost their entire length, forming a more or less tight bun-

dle; stalk of gills at least twice as long as wide on narrow portion (fig. 79A–C) . 48

Gill branches slightly divergent on basal portion and forming a fan or scoop-shaped structure with concavities formed by the two gills facing each other; stalk of gills shorter than wide, or at most 1.5 times as long as wide on narrow portion 50

48. Stalk of gill very elongate, about five times as long as wide on narrow portion (fig. 79A–C); branches forming extremely tight bundle (Ecuador) ..... *zumbahuae*

Stalk of gills shorter, not more than three times as long as wide (fig. 70D–G, I); branches of gills forming a less compact bundle .. 49

49. Platelets of thorax arranged in small groups widely separated from other such groups (fig. 71C, F); facial trichomes usually slender; all primary gill branches only very slightly diverging from direction of longitudinal axis of basal stalk (fig. 70D–G, I); terminal branches in most cases branching off at considerable distance from basal trunk; cocoon with coarse mesh, distinct apertures between strands (fig. 70A, B) (Venezuela and Colombia) ..... *ortizi*

Platelets on thorax very numerous, in many specimens forming clusters but these in most cases connected to other such clusters (fig. 74I); facial trichomes usually stout (fig. 74A); dorsal inner primary branch of gills directed mediad, distinctly diverging from direction of longitudinal axis of basal stalk (fig. 74B–E), branches in most instances branching off close to basal trunk; cocoon tightly woven, threads delicate, no apertures present (fig. 73C) (Colombia and Ecuador) .... *multituberculatus*

50. All ramifications of gill branches extremely close to base of gill; stalk of gills shorter than wide (fig. 64N, Q, U) (Peru) ... *awa*

Ramifications of gill branches distinctly remote from base of gill; stalk of gills 1.5 times as long as wide in narrow portion (fig. 63B–E, G) (Ecuador and Venezuela) ....*flabellus*

51. Gills each with medium-size branches of subequal length, except 12th and 15th with conspicuously projecting branches at least twice as long as remaining branches (fig. 85A–D); head and thorax virtually without platelets (S Chile) ..... *shannoni*

Gills different; head and thorax in most species with from few to numerous platelets .. 52

52. Gill branchings never trichotomous; cocoon loosely woven, with conspicuous apertures 53

Gills with some branchings dichotomous and others trichotomous; cocoon tightly woven, without conspicuous apertures 54

53. Gills with branches 1 and 18 arising from primary branches very close to trunk of gill; branch 14 arising dichotomously together with branch 13 (fig. 88A–C, E) facial and dorsocentral trichomes hairlike; abdominal sternite V only with 2 + 2 hooks (fig. 88K) (Colombia and Venezuela) ....*destitutus*

Branches 1 and 18 arising from primary branches at considerable distance from base; branch 14 arising separately on primary branch below trichotomous branching giving origin to branches 11, 12, and 13 (fig. 66A–D); facial and dorsocentral trichomes in shape of spinelike seta; abdominal sternite V with the usual 3 + 3 hooks (Colombia) ..... *paramorum*

54. Branches of each gill arranged in two or three distinct groups of closely spaced units placed side by side, the individual groups often converge near their apex in lateral view (figs. 45A, B, 48A, C) 55

Branches of gill not arranged as above or, if seemingly so, individual groups not converging towards apex, in lateral view.. 56

55. Branches of each gill arranged in two groups (fig. 45A–H) (Patagonian Andes and Argentina) ..... *antarcticus*

Branches of each gill arranged in three groups (fig. 48A, C, D, G) (Patagonian Andes and central Chile) ..... *trifidus*

56. Branches of each gill arranged in two loose groups, subparallel within each group . 57

Branches of each gill not arranged in two groups, radiating from common center, diverging 59

57. Branches of gill almost perpendicular to longitudinal axis of body of pupa, forwardly bent only on their apical portion (fig. 82A, D); body length 3.5 mm, cephalopterothecal length 2.6–2.9 mm (Patagonian Andes and central Chile) ..... *fulvescens*

Branches of gills forming a rakelike structure, with only a short basal portion of branches perpendicular to longitudinal axis of body of pupa, the greatest part of the total length of branches directed forward (figs. 42A, 50A) 58

58. Platelets of head and especially thorax extremely few in number (fig. 42C, E), thorax appearing polished (Patagonian Andes) .. ..in part *rufidulus*

Platelets of head and thorax more numerous; thorax appearing distinctly granular (fig. 50B, K) (Patagonian Andes) ... *femineus*

59. Length of body 5 mm, cephalopterothecal length 3.2–3.6 mm (Patagonian Andes) .. .. *brophyi*

Length of body less than 4.5 mm (cephalopterothecal length less than 3.1 mm) .. 60

60. Primary branches of gills conspicuously thickened (figs. 82C, G–I) (central Chile, El Canelo) ..... *fulvescens* in part
Primary branches of gills not conspicuously thickened 61

61. Head and thorax with very numerous platelets, surface of thorax appearing rough (fig. 58C, E) (central Chile) ..... *luispenai*
Head and thorax with few platelets, surface of thorax appearing polished 62

62. Gills blackish (Patagonian Andes) .... in part *rufidulus*
Gills light colored (Patagonian Andes and central Chile) ..... *marginalis*

The species *kuscheli* and *vianamartinsi* are not included in the above key. *Gigantodax kuscheli* is known only from the pharate pupa and cannot be placed with certainty in our key. Nonetheless *kuscheli* is the only species found on the Juan Fernandez Islands, and an eventual comparison of material with the description will serve to accurately identify the species. *Gigantodax vianamartinsi* belongs to a large complex of species with filiform gill branches that are exceedingly difficult to identify. We did not have any pupal material of this species before us. Based on the original description it is very close to *paramorum*. We do not know the pupa of *bolivianus*.

Larvae

1. Cephalic apotome widest near middle (fig. 16E); antenna much shorter than stem of cephalic fans; their basal segment at most half as long as second, or even shorter; third segment not longer than second (figs. 16G, H, 22C); median tooth of hypostomium extending conspicuously beyond level of apex of corner teeth (figs. 16J, K, 22G); mandible with 16–20 marginal serrations (figs. 16M, N, 22D) 2
Cephalic apotome widest just before posterior margin; antenna in most cases as long as or longer than stem of mouth fans, their basal segment as long as or longer than second and third segment; median tooth of hypostomium extending or not beyond level of apices of corner teeth; mandible with varied number of marginal serrations 3

2. Gill histoblast clearly showing branching; crochet ring with approximately 135–190, with 25–40 hook rows (Patagonian Andes) ... . *igniculus*
Gill histoblast not showing branching; crochet ring with approximately 105 rows of hooks of 16–20 hooks each (Patagonian Andes) ..... *carmenae*

3. Hypostomium with median tooth distinctly projecting beyond level of apices of corner teeth (figs. 4N, 7J, 12R, S, 108D); line connecting apex of median tooth to apex of fourth lateral tooth not intersecting any other tooth 4
Hypostomium with median tooth in most species not projecting beyond level of apices of corner teeth; if thus projecting, then line connecting apex of median tooth to apex of fourth lateral tooth intersecting one or several teeth situated between them 10

4. Hypostomium with first intermediate teeth projecting beyond level of apex of corner teeth (figs. 7J, 11H, I); gill histoblast showing many convoluted slender gill branches (figs. 4Q, 7M, 11J) 5
Hypostomium with corner teeth projecting beyond level of apex of first intermediate teeth (figs. 103L, 108C, D); gill histoblast showing a few stout or many convoluted, slender branches (fig. 103K) 6

5. Maximum length of mature larva more than 11 mm; maximum head width 1.1–1.4 mm 7
Maximum length of mature larva 10 mm; maximum width of head capsule 0.8 mm (N Chile) ..... *cortesi*

6. Maximum length of mature larva 18 mm; maximum width of head capsule 1.2–1.4 mm; proleg combs with 71–82 teeth; large teeth of cephalic fan rays comparatively close (fig. 7H); histoblast as shown in figure 7M (N Chile) ..... *jatunchuspi*
Maximum length of mature larva 12.0 mm; maximum width of head capsule 1.2 mm; teeth of comb of prolegs numbering 53–59; teeth of cephalic fan rays and histoblast as shown in figure 11D, J (NW Argentina, Bolivia [La Paz], and N Chile) ..... *punapi*

7. Gill histoblast with more than 20 branches, bases relatively thin (fig. 12A, U); crochet ring with 112–122 hook rows (Peru) .... *chacabamba*
Gill histoblast with 18 or fewer branches, relatively thick basally (fig. 103K); crochet ring with 120–200 hook rows 8

8. Posterolateral spots of cephalic apotome confluent ..... *clandestinus*
Posterolateral spots of cephalic apotome distinctly separated (figs. 103C, 108A) ... 9

9. Distance between posterolateral spots of cephalic apotome smaller than, or approximately equal to, transverse diameter of spots

(fig. 103C); length of mature larva ± 10 mm (E Andes of Peru) ..... *arrarteorum*

Distance between posterolateral spots of cephalic apotome larger than transversal diameter of spots (fig. 108A); length of mature larva 13–14 mm (central Andes of Argentina [San Juan]) ..... *cilicinus*

10. Antenna distinctly projecting beyond level of apice of cephalic fan stem (figs. 30C, 125E); second antennal article in most but not all species less than one-half length of first (figs. 26H, 125K, 128G, 144G) 11

Antenna not (figs. 154U, 161C) or only very slightly longer than stem of cephalic fan (fig. 142E); second antennal segment in many but not all species as long as or longer than half length of first 18

11. Second antennal segment only about one-third the length of first, and third slightly longer than first and second combined (figs. 26H, 30D–E); maximum length of mature larva not more than 6.5 mm; histoblast showing only long, slender gill branches 12

Second antennal segment between one-third and one-half as long as first, and third slightly shorter than first and second combined (figs. 91A, 125K); length of mature larva more than 6.5 mm; histoblast very different 13

12. Cervical sclerites with their mesal ends pointed, their length equal to one-third the maximum width of cephalic apotome (fig. 30C); hypostomium with median tooth not reaching level of apices of corner teeth (fig. 30K); crochet ring with 18 hooks in each row (Patagonian Andes and central Chile) ..... *minor*

Cervical sclerites with their mesal ends dot-shaped; their length equal to one-half the maximum width of cephalic apotome (fig. 26O); hypostomium with median tooth reaching level of apices of corner teeth (fig. 26M, N); crochet ring with 14–15 hooks in each row (N Chile) ..... *eremicus*

13. Third antennal segment very slightly longer than first; ratio 1:1.05–1.1 (figs. 114N, 125K) 14

Third antennal segment distinctly longer than first; ratio 1:1.2–1.4 (fig. 128F, G) 15

14. Histoblast without thin filaments (fig. 144K); crochet ring with about 90 rows of hooks; length of second antennal article 0.3 that of first (Colombia) ..... *septenarius*

Histoblast with thin filaments (fig. 125J); crochet ring with about 80 rows of hooks; length of second antennal article 0.45–0.48 that of first (Peru) ..... *abalosi*

15. Mandible with 5–6 marginal serrations (fig. 122G); perianal scales much reduced in number, restricted to area of X-shaped sclerite ..... *leonorum*

Mandible with 6–11 marginal serrations (fig. 128P, Q); perianal scales very numerous, forming complete circumanal ring (fig. 152D) 16

16. Gill histoblast showing well-developed cuticular processes on branches (fig. 114J); crochet ring with 92–100 rows of hooks (Ecuador and Colombia) ..... *misitu*

Gill histoblast without cuticular processes on branches, or if present, then obsolescent; crochet ring with 80–85 rows of hooks 17

17. Terminal sensillum 4.1 times as long as wide at base; gill histoblast basally with irregular striations (fig. 128H) (Peru) ... *cormonsi*

Terminal sensillum 8.0 times as long as wide at base; gill histoblast basally without irregular striations but with 5–9 visible branches (fig. 142Q) (Venezuela) . *bettyae*

18. Hypostomial bridge conspicuously darkened, not distinctly lighter along middle (fig. 176C); antenna as long as or slightly longer than stem of mouth fans, their second segment only slightly shorter than first; hypostomium with median tooth attaining or somewhat projecting beyond level of apices of corner teeth (fig. 176G–J); gill histoblast striated basally and with thin filaments only (fig. 176C) (Ecuador) ..... *cypellus*

Different combination of characters 19

19. Antenna distinctly shorter than stem of mouth fans (fig. 161C); and median tooth of hypostomium reaching or surpassing level of apices of corner teeth (figs. 146B, 154X, 161J, K) 20

Antenna not distinctly shorter than stem of cephalic fan, or if so, then median tooth of hypostomium falling short of level of apices of corner teeth (fig. 138S) 22

20. First and second antennal segments combined at most seven times as long as width of second segment (figs. 146M–O, 154Z); imaginary line connecting apices of corner teeth to apices of fourth lateral teeth intersecting at a wide angle; histoblast with evidence of respiratory filaments (figs. 146A, 154AA); length of larva less than 8 mm 21

First and second antennal segments combined more than seven times as long as width of second segment (fig. 161D); line connecting apices of corner teeth to apices of fourth lateral teeth intersecting at an acute angle; histoblast without evidence of respiratory filaments; length more than 8 mm (Pata-

gonian Andes and central Chile) ..... *rufescens*

21. Hypostomium with median tooth conspicuously extending beyond level of apices of corner teeth (fig. 146B); perianal scales absent (Guatemala) ..... *aquamarensis*

Hypostomium with median tooth reaching but not surpassing level of apices of corner teeth (fig. 154X); perianal scales present (Mexico) ..... *wrighti*

22. Rectal gill with numerous secondary lobules (fig. 36N); second segment of antenna 0.68–0.74 times as long as first article; median tooth of hypostomium below level of apices of corner teeth (fig. 36K) (Ecuador) .. .. *multifilis*

Rectal gill with only three simple lobes; second segment of antenna and median tooth of hypostomium with variable ratios.. 23

23. Second antennal segment 0.6–0.9 times as long as first; terminal sensillum generally 3–4.5 times as long as wide at base; if over median hypostomium tooth it is over level of corner teeth 24

Antennae with second segment 0.3–0.68 times as long as first; terminal sensillum generally 5–8 times as long as wide at base 36

24. Level of median tooth reaching apices of corner teeth or beyond (figs. 150C, 153K) 25

Median tooth distinctly below level of apices of corner teeth (fig. 46J) 31

25. Median tooth at same level of corner teeth apices (figs. 91G, 153K) 26

Median tooth surpassing level of corner teeth apices (figs. 150I, 168L) 28

26. Gill histoblast without filament branches (fig. 153J) (Venezuela) 27

Gill histoblast with filament branches (fig. 91E) (Colombia and Ecuador) .... in part *basinflatus*

27. Length of mature larva 7.8–8.5 mm, width of head capsule 0.8 mm; mandible with 7–9 marginal serrations; gill histoblast not striated and with about seven branches (fig. 153J) (Venezuela) ..... *corniculatus*

Length of mature larva about 5.0 mm, width of head capsule 0.5 mm; mandible with 1–2 marginal serrations; gill histoblast striated and with three branches (fig. 164H) (Andes of central Chile and Patagonia) .... in part *dryadicaudicis*

28. Hypostomial bridge homogeneous without light median longitudinal line 29

Hypostomial bridge with a light-colored median longitudinal line 30

29. Color of body brownish; terminal sensillum 6.0 times as long as wide at base; cephalic fans with 23–26 rays (Peru) ..... *herreri*

Color of body whitish; terminal sensillum 4.0–4.7 times as long as wide at base; cephalic fans with 28–32 rays (Venezuela) .... *impossibilis*

30. Gill histoblast with thin filaments (fig. 150D, E) (Ecuador, Colombia, and Venezuela) .. .. *cervicornis*

Gill histoblast without thin filaments (fig. 165N) (Peru and Bolivia) ... *incapucara*

31. Corner teeth not distinctly surpassing the other teeth (fig. 74N); third intermediate tooth at about same level as median tooth; almost entire body with purple hypodermal pigment (Colombia and Ecuador) .... *multituberculatus*

Corner teeth distinctly surpassing the other teeth (figs. 40I, J, 46E, J, 72A, D); third intermediate tooth generally below level of the median tooth; body color whitish to light greenish-brown 32

32. Color of larva whitish; postgenal ridge lacking pigment as the recurrent struts of anal sclerite (the last difficult to perceive) (Ecuador) ..... *gracilis*

Color of larva pale grayish-brown or light greenish-brown, postgenal bridge and recurrent struts of anal sclerite well pigmented 33

33. Hypostomial bridge with a whitish median longitudinal stripe (fig. 83A); crochet ring with 82–96 rows of 15–20 hooks each. 34

Hypostomial bridge evenly pigmented; crochet ring with 78–125 rows of 15–21 hooks each 35

34. Third antennal segment 1.20–1.25 longer than first segment (fig. 78C, D); mandible with 5–8 marginal serrations (fig. 78E) (Ecuador) ..... *laevigatus*

Third antennal segment 1.4–1.6 times longer than first segment; mandible with 7–11 marginal serrations (Patagonian Andes) .. .. *fulvescens* + in part *chilensis*

35. Maximum length 6.5–7.5 mm; width of cephalic capsule 0.65–0.75 mm (Patagonian Andes and central Chile) .... *chilensis* + *marginalis* + *luispenai* + *rufidulus* in part *femineus* and *trifidus* (Colombia and Venezuela) ... *ortizi*

Maximum length 8.0–10.0 mm; width of cephalic capsule 0.8–0.9 mm (Patagonian Andes) .. *antarcticus* + *brophyi* + *femineus* (Patagonian Andes and central Chile) ... *trifidus* (Islas de Juan Fernandez) ... *kuscheli*

36. Antenna with second segment at most 0.33–

0.36 times as long as first (fig. 138T); terminal sensillum about 6.0–6.3 times as long as wide at base (NW Argentina) ..... *horcotiani*

Antenna with second segment from 0.37 to 0.68 or more times as long as first (figs. 86A, 136A); terminal sensillum in most cases five, occasionally up to six times as long as wide at base (fig. 86B) 37

37. Antenna very slender, first and second segments combined about 18 times as long as width of second segment (fig. 136A); cephalic fan with 20–24 large rays; mandible with 8–11 marginal serrations (fig. 136G, H) (Colombia) ..... *siberianus*

Antenna somewhat stouter, first and second segments combined not more than 15 times as long as width of second segment (figs. 86A, 98A, O, 164E); cephalic fan with 22–35 or more large rays; mandible with 5–10 marginal serrations 38

38. Apex of median tooth of hypostomium approaching level of apices of corner teeth (figs. 91G, 164F) 39

Apex of median tooth of hypostomium falling considerably short of level of apices of corner teeth (figs. 86G, 117A) 43

39. Lines connecting apices of corner and fourth lateral teeth meeting at a wide angle (±130°); mandible with third preapical tooth longer than apical tooth and with only two distinct marginal serrations (fig. 164I); histoblast without filaments (fig. 164H) (central Andes of Chile and Patagonia) ..... *dryadicaudicis*

Imaginary lines connecting apices of corner and fourth lateral teeth meeting at a narrower angle (95–110°); mandible with third preapical tooth shorter than apical tooth and with 8–11 marginal serrations (fig. 91J); gill histoblast with filaments (figs. 67A, B, 91E) (Colombia and Ecuador) 40

40. Gill histoblast basally showing only filaments 41

Gill histoblast basally with irregular striations and distally with thin filaments (fig. 132C) (Ecuador) ..... *vulcanius*

41. Gill histoblast with thick filaments basally and abruptly thin filaments distally (fig. 98E) (Peru) ..... *pennipunctus*

Gill histoblast with filaments becoming thin from base to apex 42

42. Gill histoblast as long as or longer than high (fig. 67A, B); third antennal segment 1.2–1.4 times longer than first .. *paramorum*

Gill histoblast shorter than high (fig. 91E); third antennal segmetn 1.43–1.67 times longer than first (Colombia, Ecuador) ... *basinflatus*

43. Gill histoblast with branches basally not fused, gradually thinner distally (fig. 86E) (Patagonian Andes and central Chile) ..... *shannoni*

Gill histoblast with branches basally thick, and becoming abruptly very thin distally (fig. 117B) (Colombia) ..... *brevis* + *wygodzinskyi*

Larvae are unknown for the following species: *araucanius, awa, bolivianus, conviti, flabellus, incomitatus, mariobordai, nasutus, patihuaycensis, praealtus, viannamartinsi,* and *zumbauae.* Not included because of scarcity of material is *destitutus.*

DESCRIPTIONS

cortesi group

DIAGNOSIS: Differs from other species groups by the absence of calcipala; females with a wide frons and obsolescent subbasal tooth intarsal claw; frontal, facial and labral trichomes present; second antennal segment of larva longer than first; recurrent struts conspicuously well developed.

FEMALE: Overall color black, frons wide (figs. 8A, B), frontal angle 110–130°, median sulcus scarcely evident; eye and ommatidia smaller than in other *Gigantodax* species. Fronto-ocular triangle higher than wide (figs. 1B, 5B, 8E). Antenna with scape and pedicel globose, with long hairs; first flagellomere elongate (figs. 1C, 5C, 8G). Maxillary palp with basal article stout; sensorial vesicle small (figs. 1D, 5D, 8M). Mandible and maxilla obsolescent (figs. 1E, F, 8H–L). Hypopharynx short, with basal portion of cibarium smooth, not sclerotized (fig. 5F). Pronotal sclerites large. Scutum and scutellum flattened with erect and recumbent hairs. Wing with fumose membrane and big microchaetae. C with comparatively fewer but stouter spines than other *Gigantodax* species; R_1 without spines but with numerous placoid sensilla. Furcasternum with wide median arm (fig. 8P), and katepisternum comparatively elongate (fig. 9I). Hind coxa with long hairs; first posterior tarsomere shorter than tibia; calcipala and pedisulcus lacking (figs. 1G–J, 8S, T, 9L, M). Claws without transverse sulcus, basal tooth

very short (figs. 1J, K, 8U). Abdomen stout, eggs well developed at eclosion (plentiful). Abdominal tergal plates with sclerotized area four times wider than high and pleural area reduced (fig. 5G); gonapophyses with length of distal border normal (figs. 1L, 5I). Genital fork with median branch wide basally, becoming thin toward apex; lateral arm wide and lateral projection sclerotized (figs. 1N, 8V, X). Spermatheca pyriform (fig. 8V), not enlarged. Cercus subrectangular with straight border and short paraproct (figs. 1M, 8W).

MALE: Color as in female. Eye with interocular space on frons as wide as ommatidial diameter (fig. 2A), with small ocellar triangle generally higher than wide, and ocelli leaving space among them. Occipital area wide (fig. 9C). Head in front view subglobular in shape; clypeus at base about as wide as high (fig. 9A). Antenna, maxillary palp, wing, and legs shaped as in female. Basimere subpentagonal, distimere subtriangular, stout, with one or two apical hooks (figs. 2I, 5K, L, 9N). Ventral plate comparatively elongated, subovoidal in ventral view, with apical convexity widened in profile (figs. 2M–O, 5K, 9C–P). Median sclerite with posterior branches relatively shorter, straight, and thick (figs. 2M–P, 9P). Endoparamal organ with short apical hooks (figs. 2Q, 9Q). Aedeagus membranous, with few spinules.

PUPA: Cocoon with mesh threads thick, covering body totally (figs. 3A, 6A). Gills arborescent, with stout branches and abundant thin filamentous branches numbering 55–190 (figs. 3A–C, 6A–D, 10A–F). Head and thorax with abundant platelets. Head with clypeal, labral, and facial trichomes. Clypeus comparatively thinner than in other *Gigantodax* species. Thorax with elongated trichomes, not hooked distally as some frontoclypeal trichomes. Tergite I with 6 + 6 similar sized trichomes; hooks of pleurite IV–V implanted in sclerotized plates; sternite VI with 3 + 3 and VII with 2 + 2 hooks. Terminal segments with setae looped or spiraled, occasionally twisted (fig. 4B).

LARVA: Body cuticle with small single hairs implanted in a dark spot (fig. 4E). Cephalic apotome widest near base (figs. 4D, 7A, B). Antenna with second segment larger than first (figs. 5F, 8D, 12O). Terminal sensillum not elongated (ratio length/width = 3.2–3.6:1 (fig. 4G). Antenna shorter than stem of cephalic fan. Mandible with 15–25 marginal serrations (figs. 4I–L, 7F, G, 12E, F). Maxillary palp elongated (figs. 4M, 7I, 12G). Hypostomium with 10–25 setae on each side (fig. 7J); median tooth and first intermediate teeth longer than corner teeth.

All these characters and some others cited in the description provide good reasons for considering this as a group, independent from the other major clades of *Gigantodax*.

The sister-group is the *igniculus* group, which has in common with the *cortesi* group the high number of filamentous terminal branches (a character that also exists in *multifilis*), the elongated median tooth and also the fourth lateral tooth of hypostomium (a character also present in three species of the *cilicinum* group), as well as the large number of marginal serrations on the mandible, and the second segment of antenna longer than first in larvae, and the reduced sensory vesicle of maxillary palp in the female.

The *cortesi* group has four species: *cortesi, jatunchuspi,* and *punapi* are well known, represented by all the stages; *chacabamba* is known only by pharate pupae and larvae, and is tentatively included here because of the resemblance in these stages. Among the well-known species of the group, *cortesi* shows evident differences based especially in the morphology of pupal gills; *jatunchuspi* and *punapi* are very similar species with similar pupal gills.

DISTRIBUTION: High plateau of Andes (Puna area) from northern Chile, northwestern Argentina, Bolivia to central Peru.

Gigantodax cortesi, new species

Figures 1A–O, 2A–Q, 3A–I, 4A–Q

DIAGNOSIS: Very close to *jatunchuspi* and *punapi* but differentiated by the pupal gill having five primary branches.

DESCRIPTION: *Female.* Wing length 4.3 mm. Head blackish. Eye, antenna, and maxillary palp black, with silver pollinosity. Hairs of occiput, frons, antenna, and maxillary palp black and elongate; hairs of occiput from golden to black; metanotum and pleuron with silver pollinosity. Legs and wing veins dark gray brown to black. Decumbent setae of scutum golden, erect setae black. Setae of leg,

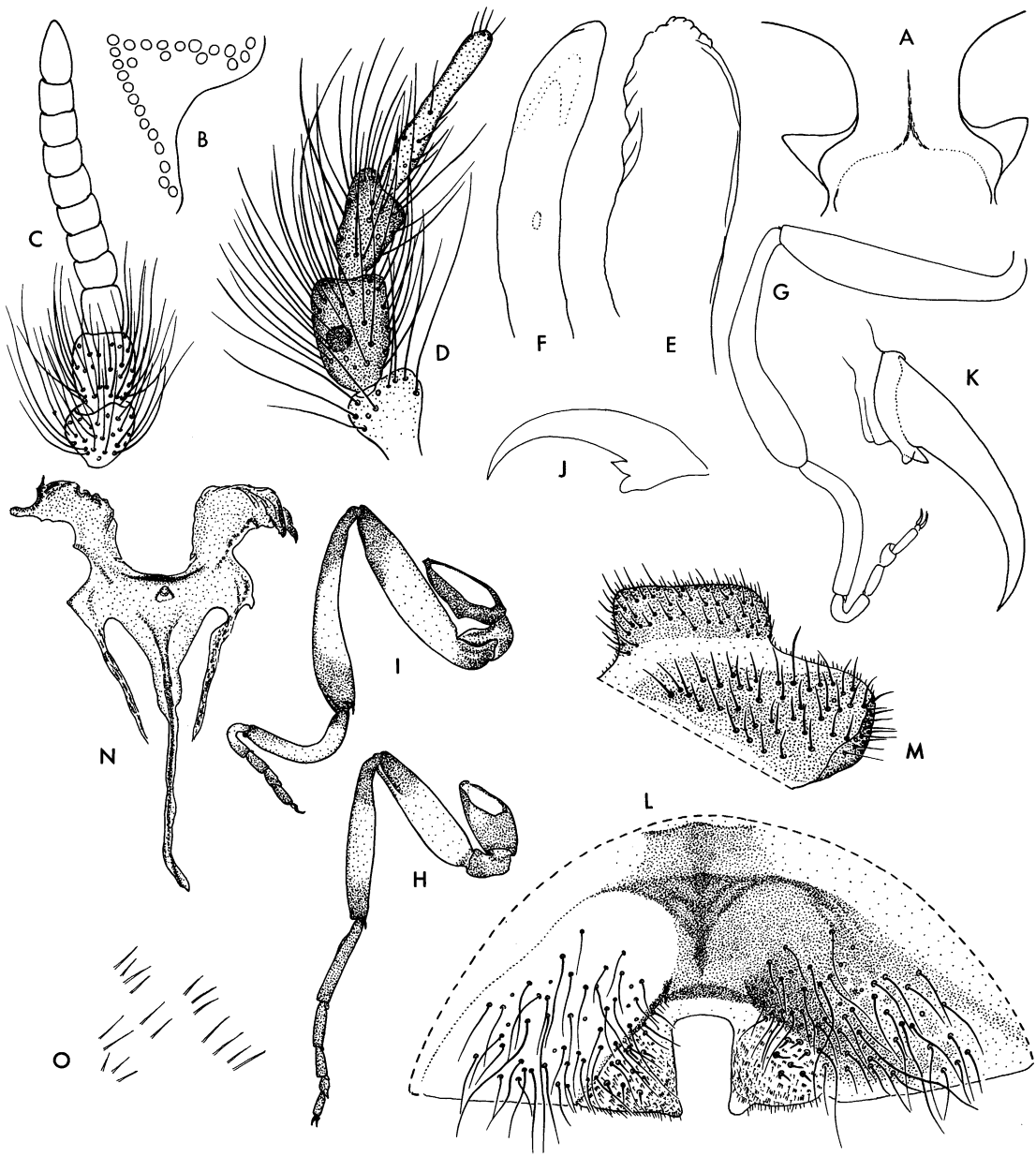

Fig. 1. *Gigantodax cortesi.* Female. **A.** Frons. **B.** Fronto-ocular triangle. **C.** Antenna. **D.** Maxillary palp. **E.** Distal portion of mandible. **F.** Distal portion of maxilla. **G, H.** Hind leg. **I.** Foreleg. **J, K.** Claws. **L.** Eighth sternite and gonapophyses. **M.** Cercus and paraproct. **N.** Genital fork. **O.** Microstructure of spermathecal wall.

wing, and abdomen from brown to black, according to the light. Abdomen black dorsally to dark gray ventrally. Frons wide, frontal angle 110° with small median sulcus (fig. 1A). Fronto-ocular triangle as in figure 1B. Antenna with basal articles stout, with long setae (fig. 1C). Maxillary palp as shown in figure 1D; sensorial vesicle approximately one-fourth as wide as basal article; sensorial vesicle shape as in *punapi.* Mandible and

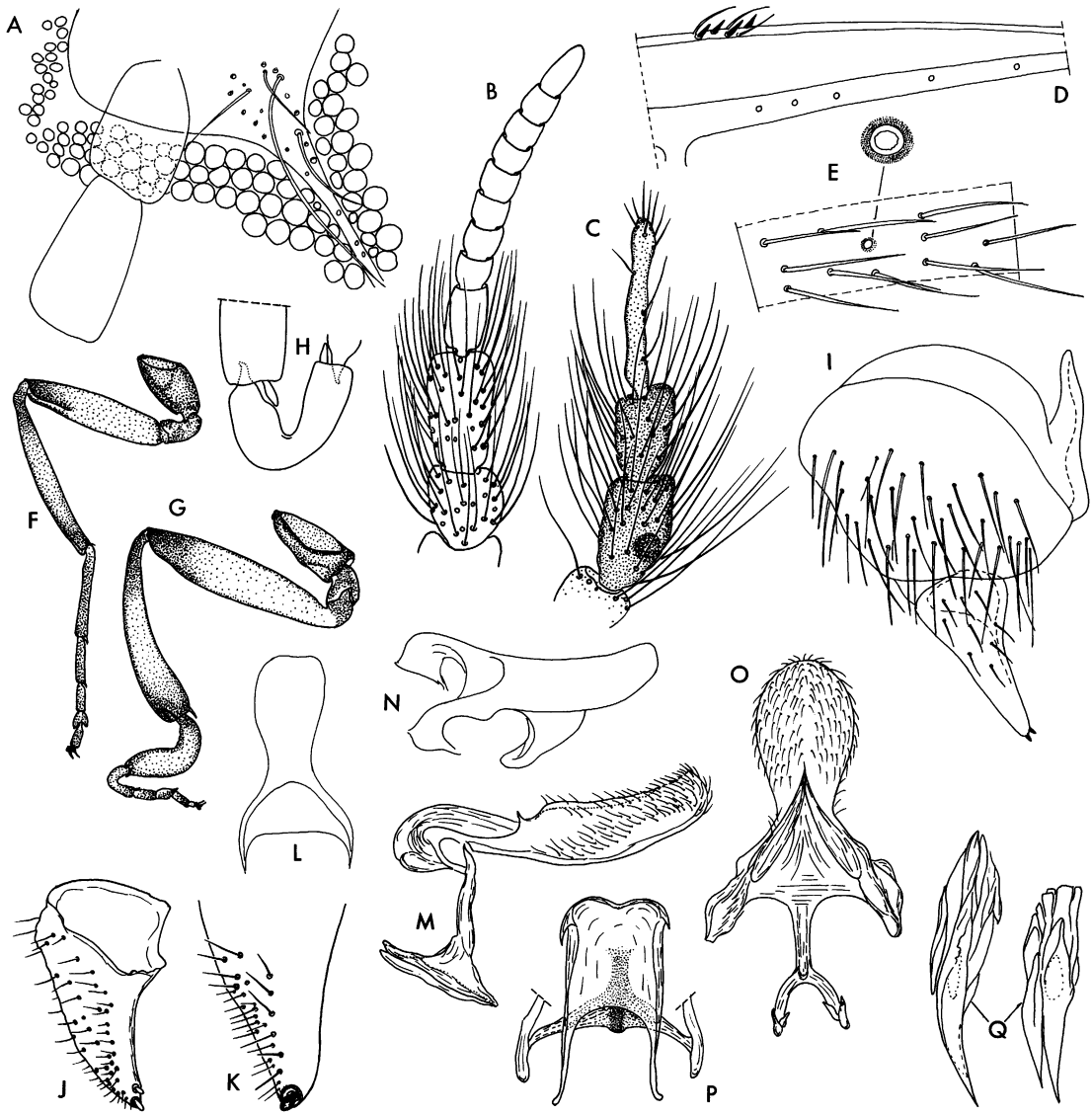

Fig. 2. *G. cortesi.* Male. **A.** Portion of head, with fronto-ocular triangle and relictual frons. **B.** Antenna. **C.** Maxillary palp. **D.** Anterior portion of wing, with location of sensilla. **E.** Portion of R_1, with setae and sensillum. **F.** Foreleg. **G.** Posterior leg. **H.** Distal portion of basitarsus, with second tarsal segment. **I.** Basimere and distimere. **J.** Distimere, different view. **K.** Different distimere. **L.** Ventral plate. **M.** Ventral plate and median sclerite, lateral aspect. **N.** Ventral plate in different position. **O.** Ventral plate and median sclerite, dorsal aspect. **P.** Median sclerite. **Q.** Endoparameral organ.

maxilla without teeth (figs. 1E, F). Wing as in male. Shape and arrangement of fore- and hindleg segment as shown in figures 1H, I. Claws with small basal tooth (fig. 1J, K).

Eighth sternite strongly sclerotized with about 50 + 50 setae; gonapophyses with 7 + 7 setae and internal border with subparallel sides (fig. 1L). Paraproct short and cerci subrectangular with distal border straight (fig. 1M). Genital fork with medial branch wide at base (fig. 1N). Spermatheca subovoid, wall with spines interiorly as shown in figure 1O.

Male. Wing length 3.7–3.9 mm. Color of the head, thorax, abdomen, and appendages

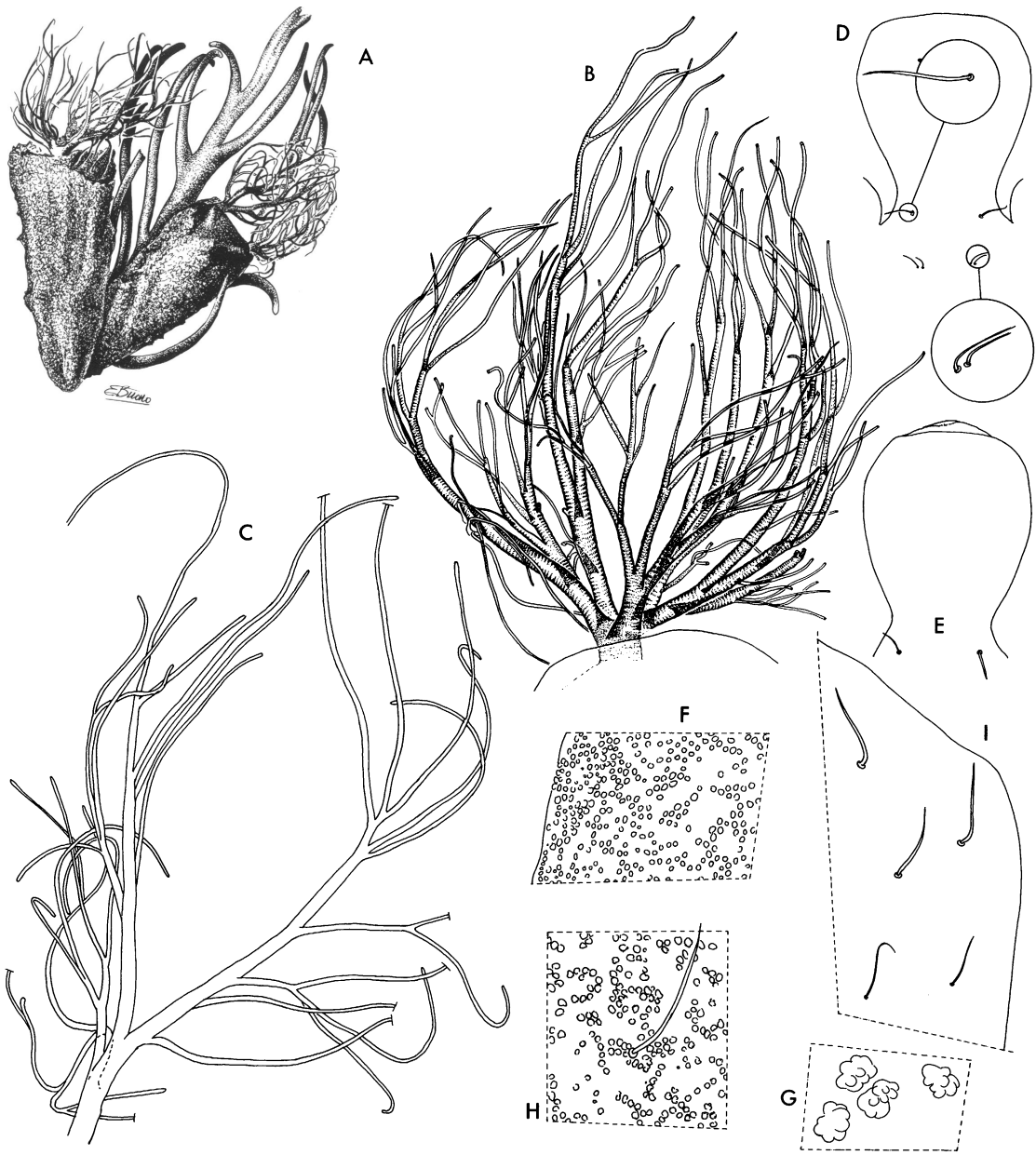

Fig. 3. *G. cortesi.* Pupa. **A.** Pupae on aquatic plant. **B.** Gill. **C.** Portion of gill. **D.** Frontoclypeus, female with trichomes in detail. **E.** Frontoclypeus of male. **F.** Platelets of frontoclypeus. **G.** Platelets, higher magnification. **H.** Trichome of thorax, with platelets. **I.** Portion of thorax, with trichomes.

as in the female. Interocular space as wide as a small ommatidium (fig. 2A). Antenna and maxillary palp as shown in figure 2B, C. Sensorial vesicle of maxillary palp wide as one-third of basal article. Wing with spines and setae on C as shown in figure 2D. Sc with hairs disposed along one row. R_1 without spines; R with abundant hairs disposed in several rows and with peculiar sensilla (fig. 2D, E). Shape, proportion, and arrangement of pigmentation of segment of fore- and hind-legs as shown in figure 2F, G. Distimere with

Fig. 4. *G. cortesi.* **A.** Chaetotaxy of abdominal tergites I and II of pupa. **B.** Portion of sternite VI, VII, and VIII, with hooks and intersegmental membrane of pupa. C–Q. Larvae. **C.** Larva, side view. **D.** Cephalic apotome. **E.** Setae of integument, with pigmented areas. **F.** Antennae. **G.** Terminal sensillum of antenna. **H.** Teeth of rays of cephalic fan. **I–K.** Apex of mandible. **L.** Mandibular serrations. **M.** Maxillary palp. **N.** Teeth of hypostomium. **O.** Cervical sclerites. **P.** Lateral sclerite of proleg. **Q.** Gill histoblast.

one or two apical hooks (fig. 2I, J). Ventral plate and median sclerite as shown in figure 2N–P. Endoparameres with strong apical hooks (fig. 2Q).

Pupa. Cocoon gray brown, mesh threads thick, totally covering the crisalid body, not perceptible externally. Maximum length of gill branches 1.5 mm, cephalopterothecal

length 4.0–4.4 mm. Length of body 4.0 mm. Gill arborescent with five main branches arising from a short basal stem. Main branches subdivided into small secondary and tertiary—or more—divisions, with approximately 100 terminal filaments (fig. 3B, C). Frontoclypeus of female and male as shown in figure 3D, E. Chaetotaxy of frontoclypeus with 1 + 1 facial and labral trichomes and in some specimens also 1 + 1 genal. Frontoclypeus and thorax with abundant rugose platelets (fig. 3F–H). Chaetotaxy of thorax as shown in figure 3I. Chaetae of abdominal tergites I, II disposed as shown in figure 4A. Chaetae of pleural and intersternal membrane with basal plate as shown in figure 4B. Chaetae of distal sternites curved.

Larva. Maximum length 10 mm. Maximum width of cephalic capsule 0.7–0.8 mm. Color pale gray brown, head light brown. General aspect of larva as in figure 4C. Cephalic apotome with positive spots, and basal spots blending posteriorly with poorly defined dark area (fig. 4D). Setae of cuticle as figured in 4E. Shape and proportions of antennal segments as shown in figure 4F. Ratio of segments I–III = 1:1.5:1.4. Terminal sensillum 3.2 times as long as wide at base (fig. 4G). Maxillary palp with 4–5 apical papillae (fig. 4M). Cephalic fans with 30–35 rays. Ray teeth as shown in figure 4H. Mandible with about 15 inner teeth, serrations as shown in figure 4I–L. Shape of hypostomium similar to that of *jatunchuspi,* with 10 setae of each side in one or two rows and 6–10 on disc. Dentition of anterior border as shown in figure 4N. Crochet ring with about 135 rows with 26–33 hooks each. Comb of proleg sclerite with approximately 35 teeth (fig. 4P). Gill histoblast as shown in figure 4Q.

HOLOTYPE: CHILE. *Parinocota:* Putre, 3600 m, Nov. 10, 1967 (S. Coscarón; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, allotype, female, 2 paratype males, 1 female paratype with pupal exuviae, abundant pupae and larvae; idem, 1 male paratype and 1 female paratype in MLP. Altos de Pacollo, Sept. 22, 1979 (S. Coscarón; MLP), 1 male larva; Pacollo 4200 m, Dec. 19, 1980 (Bobadilla; MLP), larvae.

BIOLOGICAL INFORMATION: Pupae isolated or in groups of 2–4 on *Potamogeton* leaves (fig. 3A). Preimaginal stages were collected in a small creek of the pit drainage with crystalline and cold water (with ice at sides at 4 P.M.). This species was collected with *Simulium (P.) quechuanum.* Some of the larvae were parasitized by mermithids (Nematoda).

ETYMOLOGY: Named for Dr. Raul Cortes from the University of Chile, who helped with the second author's travels in that country.

DISCUSSION: The closest species are *jatunchuspi* and *punapi,* which can be separated by the disposition of the gill branches and the small size in all stages.

Gigantodox jatunchuspi, new species

Figures 5A–L, 6A–F, 7A–M

DIAGNOSIS: The largest species of the *cortesi* group and one of the largest *Gigantodax* (wing length 5.5–6.0 mm), with pupal gill of four branches and a maximum length of 5.5–6.5 mm.

DESCRIPTION: *Pharate female.* Wing length approximately 6 mm. Overall color blackish as in *cortesi.* Frons (fig. 8A) very wide; frontal angle 130°. Fronto-ocular triangle as shown in figure 5B. Antenna with stout basal articles, with long hairs (fig. 5C). Maxillary palp darkly pigmented, with long hairs. Sensorial vesicle very difficult to perceive, small, with diameter about half of basal article (fig. 5E). Basal portion of cibarium smooth, without strong sclerotization (fig. 5F). Setae of scutum and scutellum, shape of wing and claw as in *cortesi.* Shape of legs similar to *punapi.* Abdomen shape and pigmentation as shown in figure 5G, H, with tergal and sternal plates subrectangular. Eighth sternite with approximately 60 + 60 setae; gonapophyses subtriangular with 9 + 9 setae (fig. 5I). Cercus wide with convex border and short paraproct (fig. 5J).

Male. Wing length 5.5 mm. Color and shape of body and head appendages similar to *punapi.* Ratio length/width of hind basitarsus = 4.5. Chaetotaxy of wings as in *cortesi.* Genitalia as in figure 5K, L.

Pupa. Cocoon light brown, with lead-colored shine covering entire body and gills, or only from base; body of pupa not perceptible through the cocoon. Length of cocoon 11–13 mm, maximum length of gills 5.0–6.5 mm, length of body 7.5–8.0 mm, cephaloterothecal length 4.7–4.8 mm. Gills arborescent, with six main branches with abundant subdivi-

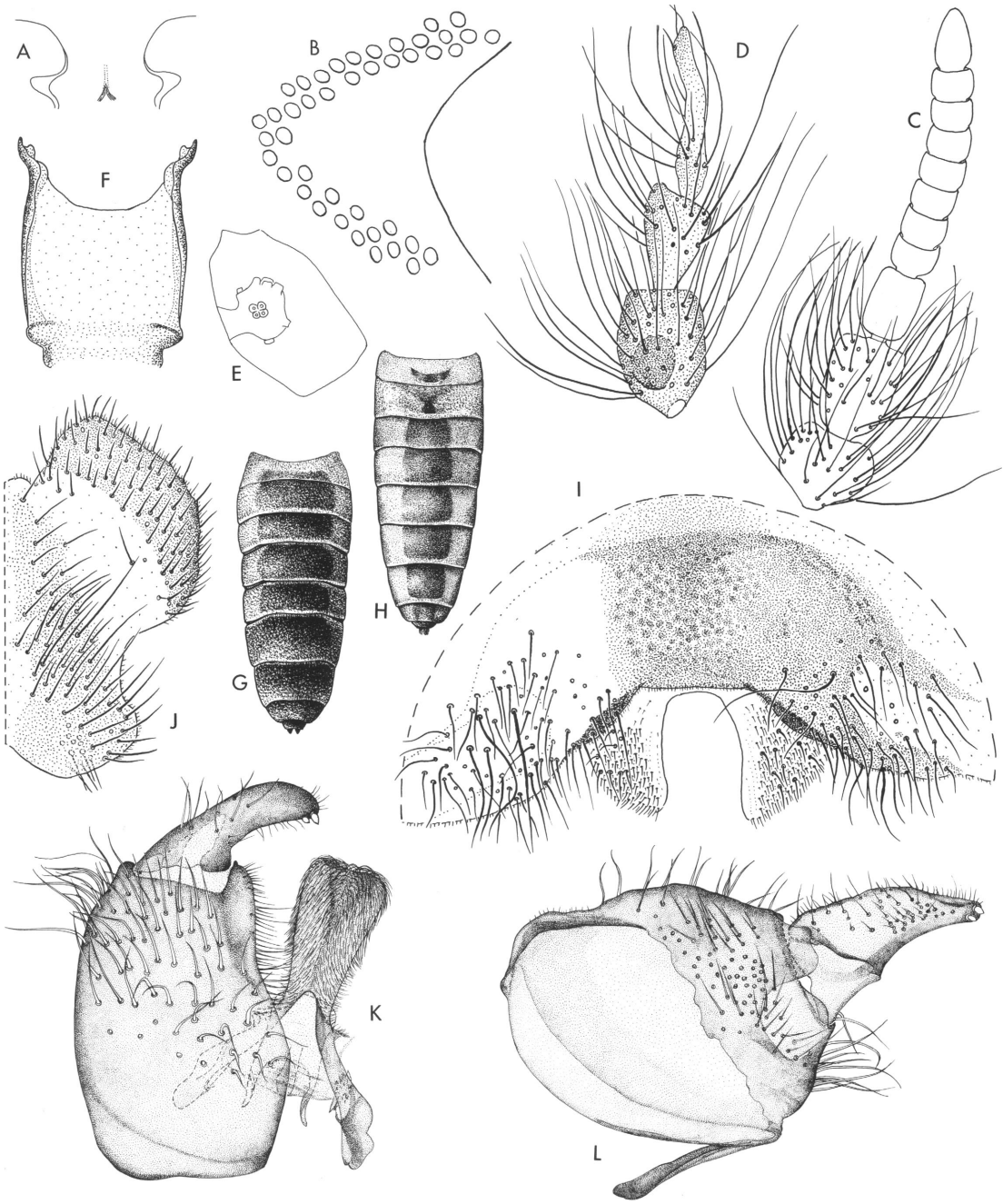

Fig. 5. *Gigantodax jatunchuspi.* A–J. Female. **A.** Frons. **B.** Fronto-ocular triangle. **C.** Antenna. **D.** Maxillary palp. **E.** Second article of maxillary palp, with sensory vesicle. **F.** Cibarium. **G.** Abdomen, dorsal aspect. **H.** Same, ventral view. **I.** Eighth urosternite and gonapophyses. **J.** Cercus and paraproct. **K.** Genitalia male in normal position. **L.** Basimere and distimere.

sions and many minor filamentous branches at base (fig. 6A–D). The second and third primary branches subdivided at short distance from base; number of terminal gill fil-

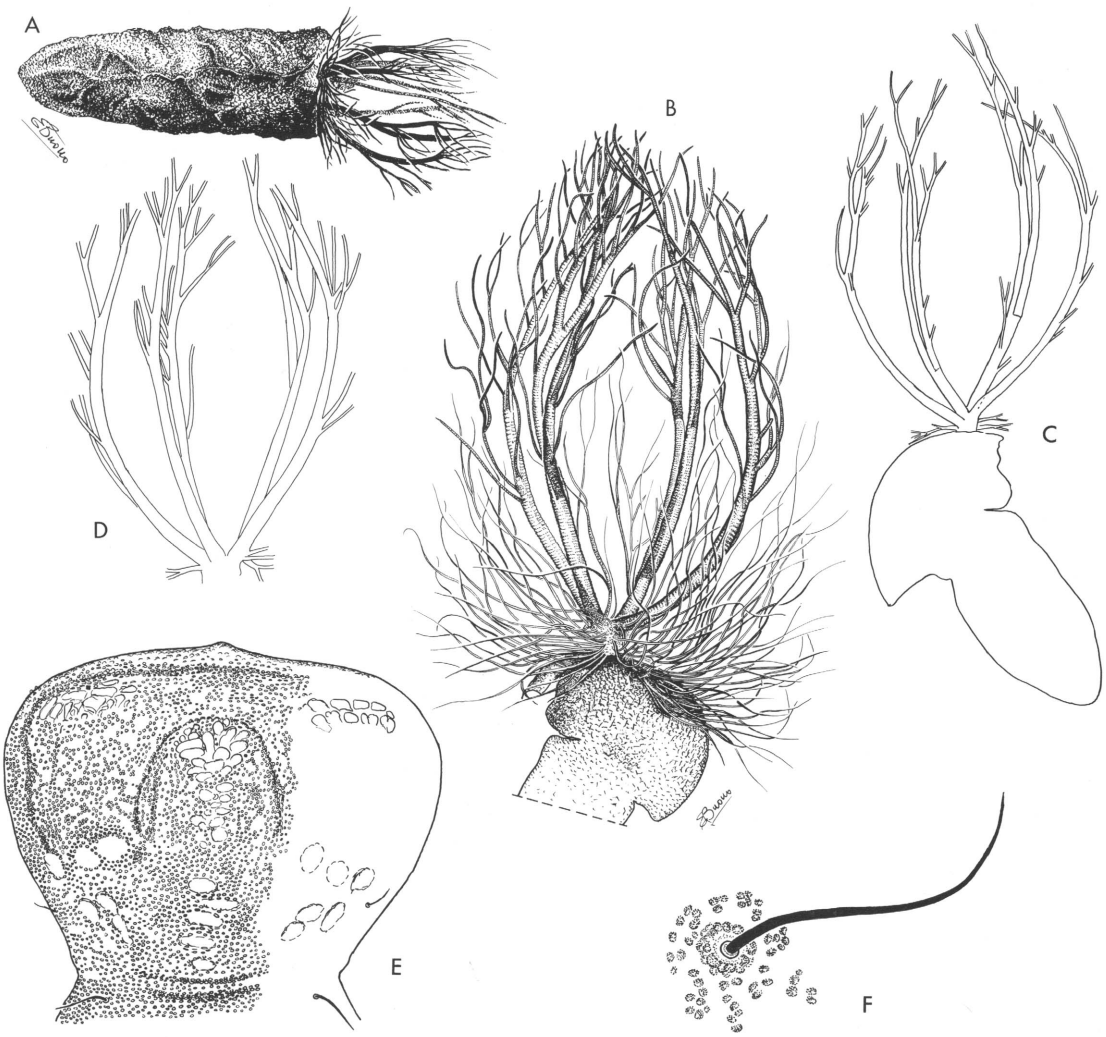

Fig. 6. *G. jatunchuspi.* Pupa. **A.** In cocoon. **B.** Portion of thorax, with gill. **C, D.** Same, schematic. **E.** Frontoclypeus of female. **F.** Facial trichome.

aments about 180; frontoclypeus and thorax with abundant platelets (fig. 6E, F). Head chaetotaxy as in *punapi,* but frontal setae smaller compared with clypeal (fig. 6E) and labral setae. Chaetotaxy of abdomen as in *punapi,* but showing 0–10 spines on the anterior border of tergite VI.

Larva. Maximum length 14 mm; maximum width of head 1.2–1.4 mm. Cephalic apotome with positive spots very evident, spaces between basal spots longer than transverse diameter of each spot (fig. 7A, B). Ventral aspect of cephalic capsule as in figure 7C. Antenna as shown in figure 7D. Ratio of segments I–III = 1:1.2:1.4. Terminal sensillum about three times as long as wide at base. Palpus elongate distally with six vesicles and abundant setae (fig. 7I). Cephalic fan with 29–33 rays; teeth of rays with larger teeth very close (fig. 7H). General aspect of mandible as shown in figure 7E. Mandible with 19–22 internal teeth and abundant mandibular serrations (fig. 7E–G). Hypostomium with 19–23 lateral setae and 23–25 setae at base of disc; median tooth very high compared with corner teeth (fig. 7K). Proleg sclerite as in

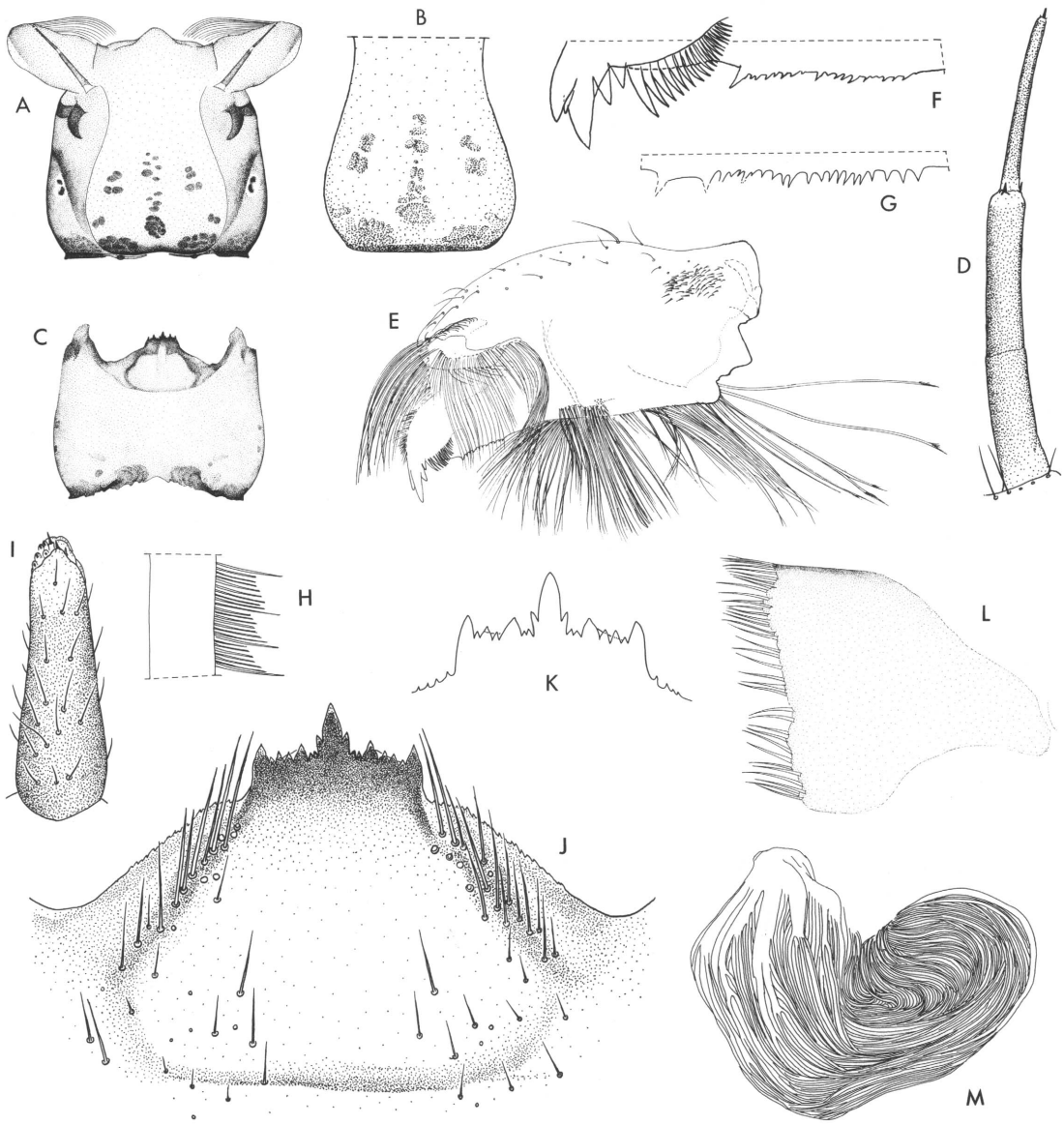

Fig. 7. *G. jatunchuspi.* Larva. **A.** Head, dorsal view. **B.** Cephalic apotome. **C.** Cephalic capsule in ventral view. **D.** Antenna. **E.** Mandible. **F.** Apical portion of mandible. **G.** Lateral serrations of mandible. **H.** Teeth of rays of mouthfan. **I.** Maxillary palp. **J.** Hypostomium. **K.** Teeth of hypostomium. **L.** Sclerite of proleg. **M.** Gill histoblast.

figure 7L. Anal sclerites with anterior scales small and very difficult to see, not closing a circle. Recurrent struts very well sclerotized. Crochet ring with 160–194 rows of 38–45 hooks each one. Gill histoblast as shown in figure 7M, more excavated dorsally than in *punapi.*

HOLOTYPE: CHILE: *Parinocota:* E of Putre, 3400 m, Oct. 13, 1967 (S. Coscarón; AMNH), pupal exuviae on slide.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 2 pupal exuviae on slides, paratypes, 1 pharate female on slide, several pupae and larvae. W of Putre, Oct.

13, 1967 (S. Coscarón; AMNH), larvae; Altos de Putre, 3600 m, Aug. 19, 1980 (N. Hickins; MLP), larvae; Altos de Pacollo, Sept. 22, 1979 (Bobadilla and Coscarón; MLP), 1 male, larvae.

BIOLOGY: Preimaginal stages were collected below stones in streams of swiftly flowing, cold and crystalline waters. The male was collected at the side of the stream. Collected in the same locality: *Simulium (P.) hectovargasi,* larva of a horsefly (*Dasybasis* sp.), and abundant larvae of Trichoptera.

DISCUSSION: This species is one of the largest Simuliidae found in the southern area of the Neotropical region. It is very close to *punapi* and *cortesi*; small differences permit one to differentiate among them as can be seen in the keys.

ETYMOLOGY: *jatun* = large, *chuspi* = fly; thus, "big fly."

Gigantodax punapi, new species

Figures 8A–X, 9A–Q, 10A–J, 11A–J

DIAGNOSIS: Very close to *jatunchuspi,* differentiated by its small size and with the main basal branches of the pupal gill not erect, but proportionately more stout.

Female. Wing length 5 mm. Overall color black, as in *cortesi.* Frons very wide (fig. 8A–C), frontal angle 130°, with median sulcus barely perceptible. Fronto-ocular triangle higher than wide (fig. 10E). Antenna as shown in figure 8G. Maxillary palp darkly pigmented, sensory vesicles difficult to perceive (fig. 8M, N). The latter small, less than one-third the diameter of the basal article, their structure as illustrated (fig. 8O). Mandible (fig. 8H, I) and maxilla (fig. 8J–L) poorly developed only with small serrulations on the apex. Furcasternum as illustrated in figure 8P, with wide median branch. Shape, proportions and arrangement of pigment of legs as illustrated (fig. 8Q–S). Calcipala not developed (fig. 8T). Claw as in figure 8U. Wing and halter as in *cortesi.* General disposition of sternite VIII, genital fork, and spermatheca as in figure 8V. Sternite VIII with 45–50 setae on each side, fully sclerotized centrally, only faintly so laterally; gonapophyses each with 7–10 setae (fig. 11A). Genital fork as illustrated (fig. 8V–X). Cercus margin from convex to almost straight, according to angle of observation (fig. 8W).

Male. Length of wings approximately 4.5 mm. Overall color black, with pigmentation pattern and distribution of setae as in *cortesi.* Head aspect as shown in figure 9A–C.

Antenna (fig. 9D), with basal articles very large; pedicellus larger than one-third the length of flagellum and over twice as wide. Maxillary palp as illustrated (fig. 9E, F). Sensory vesicle (fig. 9G) approximately one-third as wide as basal article of palp. Small fronto-ocular triangle longer than wide. Wing as in female. Katepisternum as illustrated in figure 9H, I. Shape, proportions, and arrangement of pigment of legs as in figure 9J–L; calcipala not developed (fig. 9M). Hind basitarsus six times as long as wide. Genitalia very close to those of *cortesi.* Basimere and distimere, ventral plate, median sclerite, and endoparameres as shown in figure 9N–Q.

Pupa. Cocoon tough, covering entire body and most of gills. Aspect similar to *jatunchuspi,* but smaller. Color of cocoon light brown, with lead-colored shine. Body of pupa not perceptible through cocoon. Length of cocoon 7.0–9.0 mm. Maximum length of gills 4.0 mm, of body 5.0–6.5 mm; cephalopterothecal length 3.2–3.8 mm. General aspect of gills very close to *jatunchuspi.* Disposition of main branches as in figure 10A–F. Chaetotaxy of head as shown in figure 10G–I; one pair of frontal, one pair of facial, and one or more labral setae. Chaetotaxy of abdomen typical for *Gigantodax* but pleural hooks from segments IV–VII with small sclerotized plates on base as shown in *cortesi.* Terminal hook of abdomen as shown in figure 10J.

Larva. Maximum length 12.0 mm. Maximum width of head 1.2 mm. Color as in *cortesi.* Cephalic apotome as in figure 11B. Antenna as illustrated in figure 11C, ratio of segments I–III 1:1.2–1.3:1.2–1.4. Terminal sensillum with ratio length/width = 3.6 at base. Maxillary palp (fig. 11G) with six apical papillae. Cephalic fan with 30–34 large rays, aspect of rays' teeth as shown in figure 11D, rather close to each other. Mandible (fig. 11E–F) with abundant marginal serrations. Hypostomium with 10–16 hypostomial setae arranged irregularly in each row; disc with 10–16 setae. Anterior border of hypostomium well sclerotized with apex of median tooth more than twice the length of the corner teeth (fig. 11H, I). Comb of pseudopod with 53–

Fig. 8. *G. punapi.* Female. **A–C.** Head and front in different views. **D.** Head, side view. **E.** Frontoocular triangle. **F.** Detail of eyes. **G.** Antenna. **H.** Mandible. **I.** Apice of mandible. **J.** Maxilla. **K.** Distal portion of maxilla. **L.** Apex of maxilla, different specimens and magnification. **M.** Maxillary palp. **N.** Maxillary palp, different specimen. **O.** Sensory vesicle of maxillary palp. **P.** Furcasternum. **Q.** Foreleg. **R.** Mid leg. **S.** Hind leg. **T.** Apex of basitarsus, with second tarsal segment. **U.** Claw. **V.** Genital area, with gonapophyses, genital fork, and spermatheca. **W.** Cercus and paraproct. **X.** Genital fork.

59 teeth. Crochet ring with 160–185 of 35–43 hooks each. Setae of anal area weakly pigmented and not implanted on black spots. Gill histoblast as shown in figure 11J.

Fig. 9. *G. punapi.* Male. **A–C.** Head in different views. **D.** Antenna. **E.** Maxillary palp. **F.** Maxillary palp of different specimen, not all setae shown. **G.** Sensory vesicle. **H.** Head and thorax, side view. **I.** Katepisternum. **J.** Foreleg. **K.** Mid leg. **L.** Hind leg. **M.** Apical area of posterior basitarsus, with second tarsal segment. **N.** Basimere and distimere. **O.** Basal plate. **P.** Median sclerite, lateral aspect. **Q.** Endoparameral organ.

HOLOTYPE: ARGENTINA: *Jujuy:* near Rosario de Coyaguaima, 4700 m, Nov. 4, 1968 (S. Coscarón; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, allotype female, reared, and with associated pupal skin; 3 male paratypes and 4 female paratypes, mounted on slides (some in MLP); numerous larvae

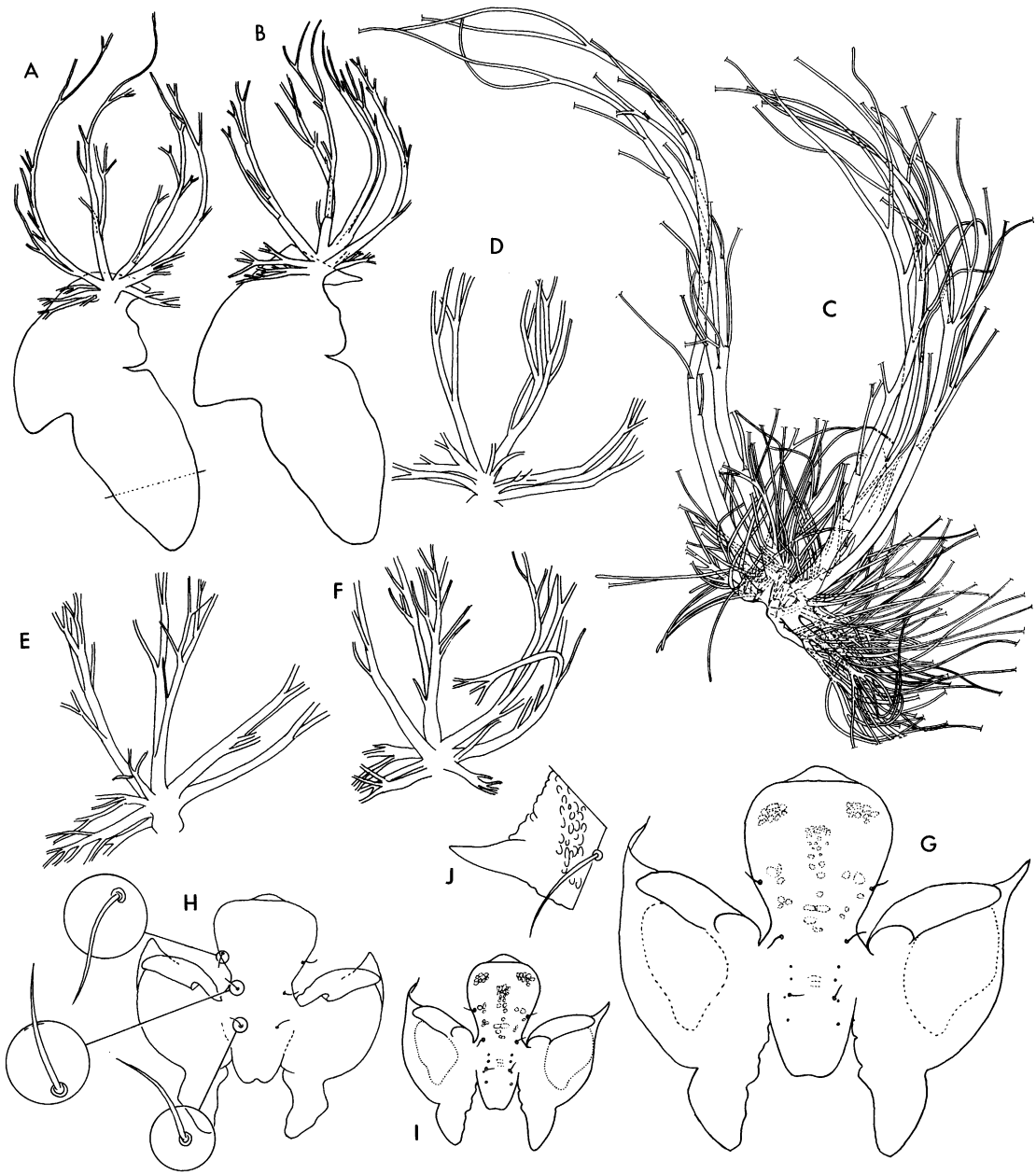

Fig. 10. *G. punapi.* Pupa. **A, B.** Thorax of pupa, with main branches of gills. **C.** Gills. **D–F.** Gills, only main branches shown. **G, H.** Cephalic sclerite of female. **I.** Same, male (different magnification). **J.** Terminal hooks.

and pupae; Rumi Mayo and Quebrada Honda, 4700 m, Nov. 4, 1968 (Coscarón; AMNH), numerous larvae. BOLIVIA: *La Paz:* road to Yungas, La Cumbre, 4500–4600 m, Oct. 28, 1968 (S. Coscarón; AMNH), larvae and pupae; ibid., 4400 m, larvae and pupae; ibid., 4200 m, Oct. 27, 1968, larvae. CHILE: *Parinocota:* Pacolla, 4200 m, Dec. 19, 1960 (Bobodilla; MLP), pupae, larvae, and pharate male.

DISCUSSION: The three species of *cortesi* group are very close, but *punapi* is closest to

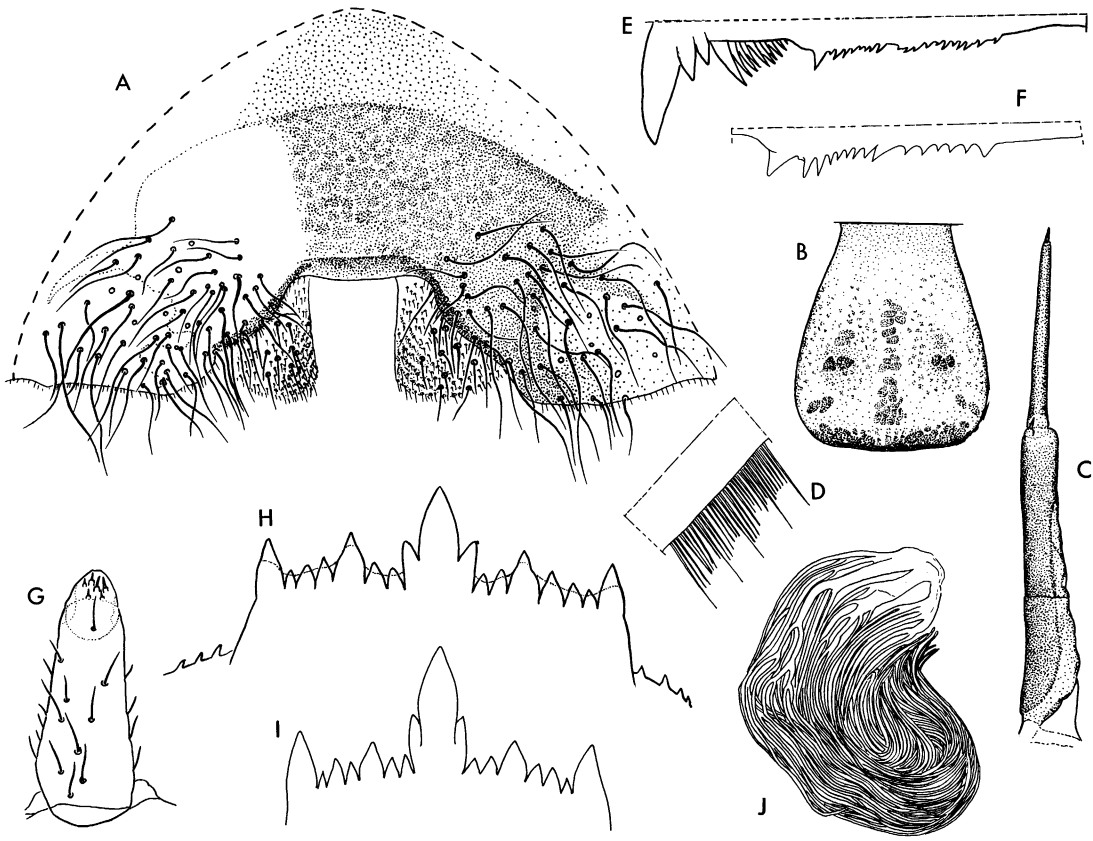

Fig. 11. *G. punapi.* **A.** Eighth sternite of female with gonapophyses. B–I. Larva. **B.** Cephalic apotome. **C.** Antenna. **D.** Detail of teeth of rays of cephalic fan. **E.** Apex of mandible. **F.** Mandibular serrations. **G.** Maxillary palp. **H, I.** Anterior portion of hypostomium. **J.** Gill histoblast.

jatunchuspi. The best characters to distinguish the species are in the pupal gills, but minor differences are also found in the other stages, as one can see in the keys.

ETYMOLOGY: The name refers to the "puna," the high plateau of the Andes in northern Chile, NW Argentina, Bolivia, and Peru, where this species lives.

Gigantodax chacabamba, new species
Figure 12A–U

DIAGNOSIS: This species is distinguished from all others of the group by filiform branches of the pupal gills that are approximately one-half the number of those seen in close relatives.

DESCRIPTION: Female and male unknown.

Pupa (pharate). Gills consisting of approximately 54 long, slender, filiform branches arising by progressive dichotomous division from five stout basal trunks inserted on a very short base (fig. 12A–F). Surface of branches minutely and uniformly dotted; cuticular projections absent. Gills at least 3.0 mm long, possibly considerably more. Apex of gill blunt (fig. 12G). Thorax with numerous platelets. Dorsocentral trichomes in form of slender, spinelike setae (fig. 12H). Other pupal characters not examined.

Mature larva. Length 11.5–12.1 mm; width of head capsule 1.1 mm. Body shape as usual for the genus; ventral papillae distinct (fig. 12I). Color of larva whitish, with very faint overall dark pigment. Head light yellowish brown, spots of cephalic apotome distinct. Posterolateral spots of cephalic apotome as wide as, or slightly wider than, distance separating them, connected at hind border of sclerite by narrow but distinct dark band (fig.

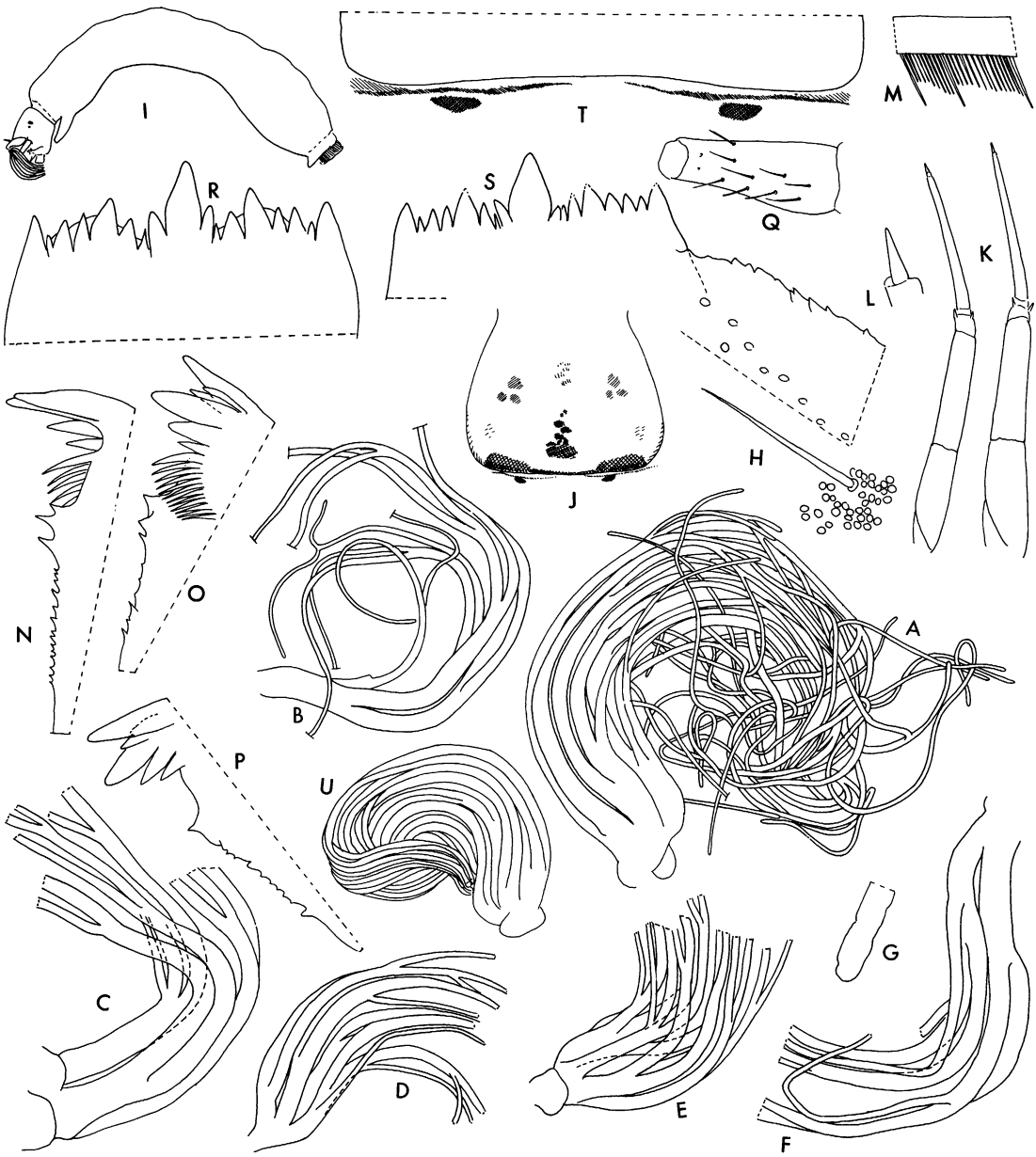

Fig. 12. *Gigantodax chacabamba.* A–H. Pharate pupa. **A.** Gill, not fully opened. **B–F.** Portions of gills. **G.** Apex of gill branch. **H.** Seta of thorax. I, J. Larva. **I.** Larva, lateral view. **J.** Cephalic apotome with cervical sclerite. **K.** Antennae. **L.** Apical sensillum of antenna. **M.** Teeth of ray of cephalic fan. **N–P.** Apex of mandible. **Q.** Maxillary palp. **R, S.** Teeth of hypostomium. **T.** Cervical sclerites. **U.** Gill histoblast.

12J). Hypostomial bridge lacking pattern elements, conspicuously contrasting with pigmented hypostomium. Antenna as long as stem of mouthfans, distinctly pigmented, third segment appearing the darkest. Shape of antenna as shown in figure 12K; ratio of segments I–III = 1:1.1–1.2:1.2–1.43. Terminal sensillum 3.5 times as long as width at

base (fig. 12L). Cephalic fans with 35–41 large rays; teeth as shown in figure 12M. Mandible (fig. 12N–P) with 10–15 inner teeth and 11–18 marginal serrations. Maxillary palpus slender, three times as long as width at base (fig. 12Q). Hypostomial teeth as shown in figure 12R, S. Median tooth projecting considerably beyond level of apices of corner teeth; line connecting apex of median tooth to apex of fourth lateral teeth not intersecting any other tooth; corner teeth projecting beyond level of apex of first intermediate teeth. Hypostomium with 13–17 lateral serrations and 8–10 hypostomial setae arranged in one or two irregular rows. Cervical sclerites consisting of 1 + 1 isolated platelets not fused to narrow transverse sclerotized bands (fig. 12T). Histoblast as shown in figure 12U; basal trunks whitish, remainder brown. Perianal scales weakly developed, difficult to perceive, discernible only in area of posterior arms of X-shaped sclerite. Recurrent struts conspicuous, well developed. Crochet ring with 112–122 rows of 25–30 hooks each. Rectal gills not examined.

HOLOTYPE: PERU: *Junin:* Tarma: Chacabamba, at road from Palcomayo to San Pedro de Cajas and Junin, 3700 m, July 15, 1965 (P. and B. Wygodzinsky; AMNH), mature larva with pharate pupa.

ADDITIONAL SPECIMENS: Eight larvae, some with early pharate pupae, same data as holotype; near Tilarnioc, km 218 of road from Oroya to Junin, in small tributary of Mantaro River, July 13, 1965 (P. and B. Wygodzinsky; AMNH), 2 larvae.

ETYMOLOGY: The specific name is taken from one of the localities where material was collected; in Quechua, *chaca* means bridge, and *bamba,* plain.

BIOLOGY: The larvae of *G. chacabamba* were found on the undersurfaces of large stones resting on the bottom of clear, moderately wide (up to one meter) streams, with a water temperature of more or less 10°C. These larvae shared this habitat with those of *G. arrarteorum.*

DISCUSSION: It is unfortunate that this most unusual species is not known from adults, and only incompletely from its pupa. The very large larvae are characterized by the structure of the hypostomial teeth, with the median tooth projecting well beyond the level of the apices of all others; this and other charcters, such as the antennal articles of similar proportions, the number of internal mandibular teeth and marginal serrations, conspicuous recurrent struts, plus the high number of filamentous gill branches, agree closely with the structures found in larvae of the species of the *cortesi* group.

igniculus group

DIAGNOSIS: This group is characterized by the hook-shaped subbasal claw tooth, elongated female gonapophyses, strong spines on the aedeagal membrane, a pupal gill with 100 filaments or more, and larvae with the first and second antennal segment very stout and frontoclypeal apotome widest near the middle.

FEMALE: Color brownish, frons narrow (fig. 17A), eye, antennae, maxillary palp, and hypopharynx as in other *Gigantodax* s.str. (except *cortesi* group). Sensorial organ of maxillary palp comparatively poorly developed (fig. 17F–I). Mandible with teeth only on internal side (fig. 17E). Scutum only with decumbent hairs. Wing with few or no spines on R_1. Calcipala well developed but not surpassing the basal third of second tarsomere (fig. 17L), subbasal claw tooth hook-shaped (figs. 17M, 178A). Genital fork with narrow lateral arms (fig. 17Q), spermatheca subglobose, normal size (fig. 17N, R). Gonapophyses elongated, internal borders sclerotized with few or no setae (fig. 17N, O).

MALE: Color as in female or slightly darker; holoptic, fronto-ocular triangle not developed; mesonotum gibbous. Ventral plate elongated with distal concavity (figs. 14I, 18H, J, 19A, E). Aedeagus with abundant and well-developed spinules, sometimes fused basally (figs. 14H–J, 18H, 19A, B, G).

PUPA: Cocoon generally well developed. Gill spherical (fig. 15A, B) to aborescent (fig. 20A–E) with stout primary branches, and generally over 100 filaments. Frontoclypeus with facial and sometimes labral trichomes (fig. 15C). Trichomes of frontoclypeus and thorax straight; distal segments of abdomen with setae looped or spiraled, occasionally twisted (fig. 21B); terminal hooks stout (fig. 15G).

LARVA: Body surface without hairs. Frontoclypeal apotome widest near middle (fig.

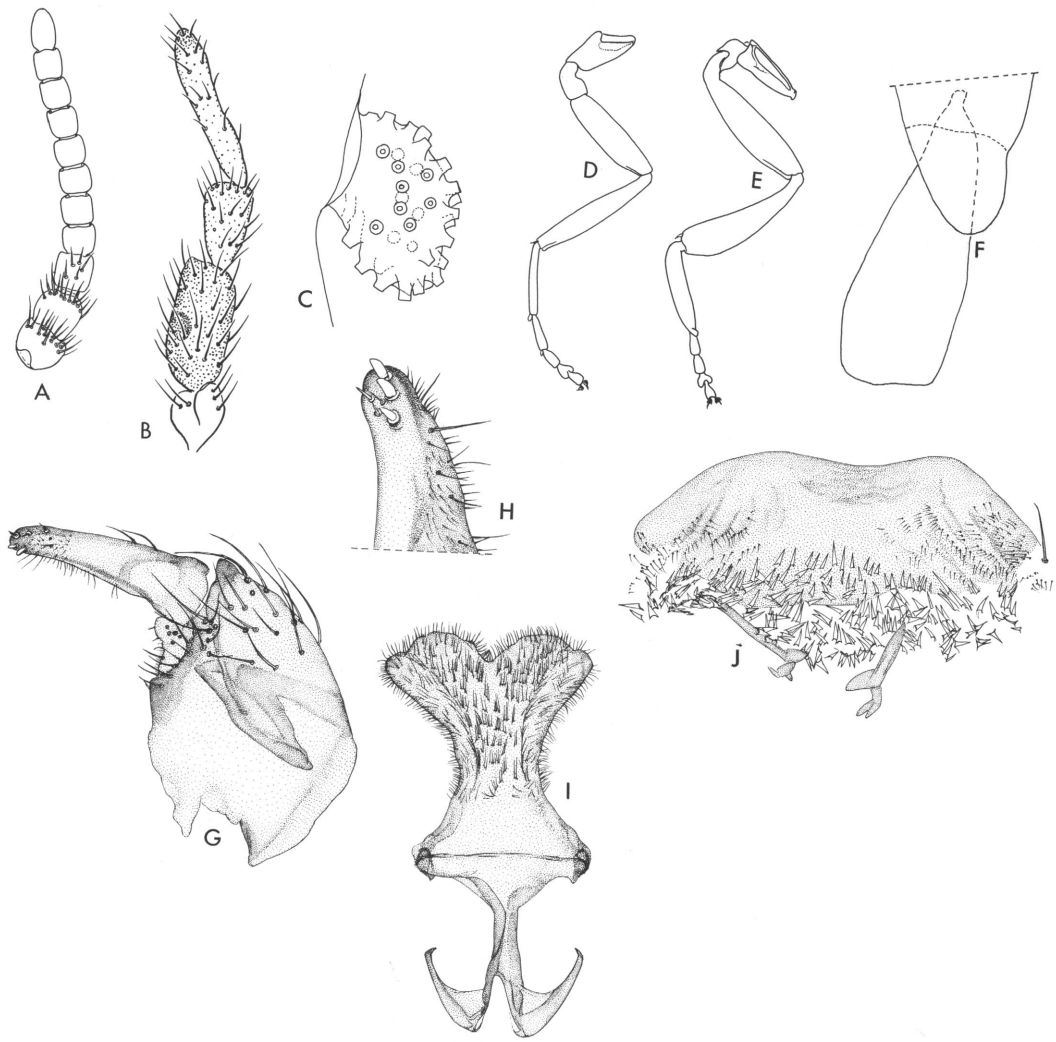

Fig. 14. *Gigantodax carmenae.* Male. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle. **D.** Foreleg. **E.** Hind leg. **F.** Calcipala. **G.** Basimere and distimere. **H.** Apex of distimere. **I.** Ventral plate and median sclerite. **J.** Spinules of aedeagus and endoparameral organ.

with setae arranged in two or three irregular rows. Spinules distinct, numerous, beginning at level of insertion of Sc on C. R_s with setae in one or two irregular rows. Fore and hind legs as shown in figure 14D, E. Fore basitarsus about 10 times, posterior basitarsus about 5 times, as long as wide. Calcipala covering slightly less than half length of second tarsal segment (fig. 14F). Genitalia as shown in figure 14G–J.

Distimere about twice as long as basimere, with two to four apical spines (fig. 14G, H). Ventral plate (fig. 14I) longer than wide, narrowed at middle. Median sclerite as shown in figure 14I. Endoparameral organ and portion of aedeagus with spinelike processes (fig. 14J).

Pupa. Cocoon small, leaving part of thorax and dorsal respiratory organs exposed (fig. 15A). Thorax on each side with a shortly stalked, spherical, darkly pigmented respiratory organ, each beset with more than 100 short respiratory filaments. Filaments not longer than diameter of spherical structure, their apices rounded (fig. 15B).

Frontoclypeus with large number of small

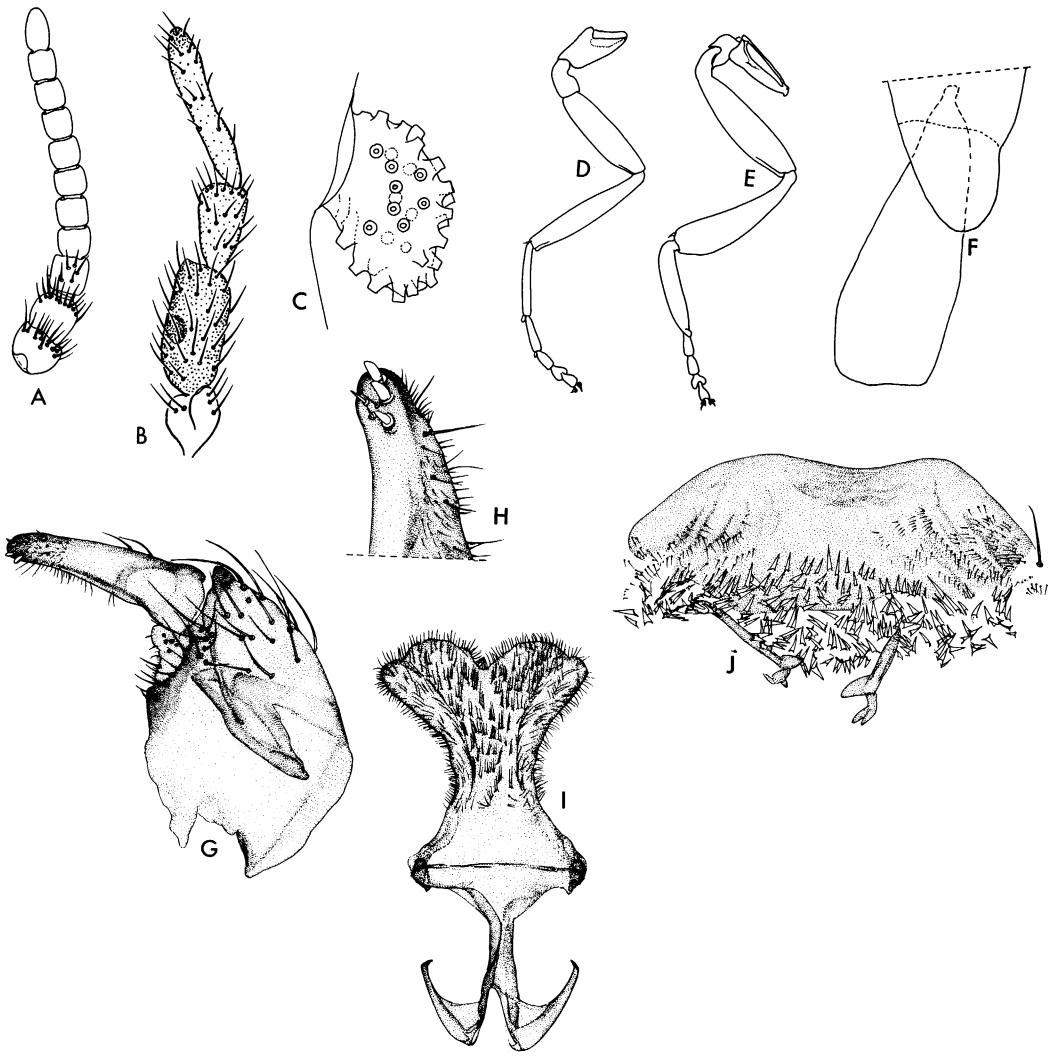

Fig. 14. *Gigantodax carmenae.* Male. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle. **D.** Foreleg. **E.** Hind leg. **F.** Calcipala. **G.** Basimere and distimere. **H.** Apex of distimere. **I.** Ventral plate and median sclerite. **J.** Spinules of aedeagus and endoparameral organ.

with setae arranged in two or three irregular rows. Spinules distinct, numerous, beginning at level of insertion of Sc on C. R_s with setae in one or two irregular rows. Fore and hind legs as shown in figure 14D, E. Fore basitarsus about 10 times, posterior basitarsus about 5 times, as long as wide. Calcipala covering slightly less than half length of second tarsal segment (fig. 14F). Genitalia as shown in figure 14G–J.

Distimere about twice as long as basimere, with two to four apical spines (fig. 14G, H). Ventral plate (fig. 14I) longer than wide, narrowed at middle. Median sclerite as shown in figure 14I. Endoparameral organ and portion of aedeagus with spinelike processes (fig. 14J).

Pupa. Cocoon small, leaving part of thorax and dorsal respiratory organs exposed (fig. 15A). Thorax on each side with a shortly stalked, spherical, darkly pigmented respiratory organ, each beset with more than 100 short respiratory filaments. Filaments not longer than diameter of spherical structure, their apices rounded (fig. 15B).

Frontoclypeus with large number of small

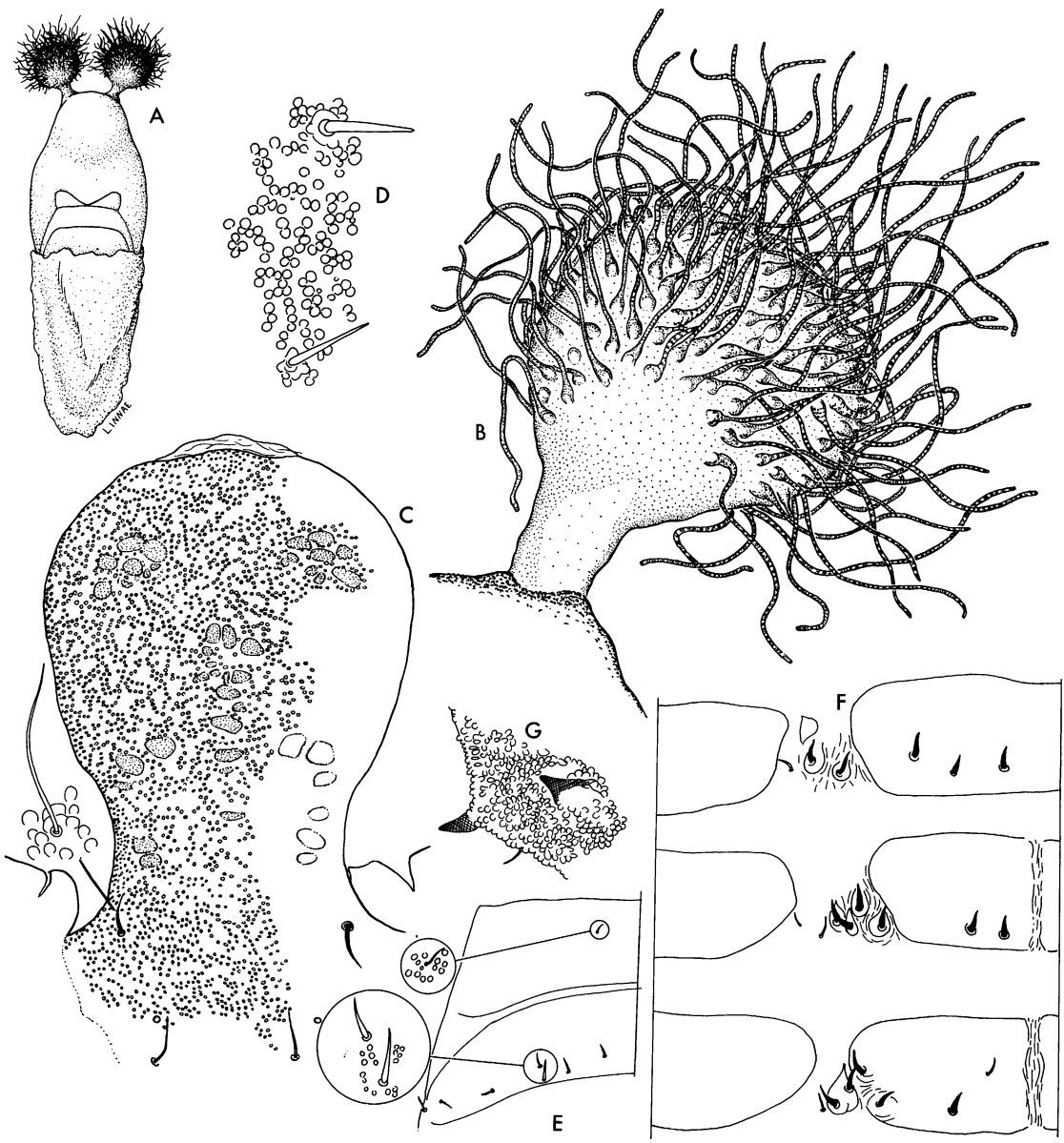

Fig. 15. *G. carmenae.* Pupa. **A.** Pupa and cocoon, dorsal view. **B.** Gill. **C.** Frontoclypeus of male. **D.** Thoracic trichomes. **E.** Chaetotaxy of abdominal tergites I and II. **F.** Sternites V, VI, and VII, showing pleural area. **G.** Apex of abdomen, dorsolateral.

glabrous platelets (fig. 15C). Facial and labral trichomes present, in form of slender setae. Thorax with strong trichomes and abundant platelets (fig. 15D). Abdomen with unusually numerous tiny platelets, giving abdomen the appearance of being strongly sclerotized. Setae of first abdominal tergite very short (15 μm), delicate, somewhat larger on second tergite (20 μm) (fig. 15E). Tergites III and IV each with 4 + 4 hooks. Setae of tergites VIII and IX simple. Sternites V and VI with 2 + 2 or 3 + 3 short hooks, VII with 1 + 1 hooks. Pleural membrane between tergites and sternites V, VI and VII with group of two to four spines at level of each pair of sclerites (fig. 15F); terminal spines of abdomen short (fig. 15G).

Larva. General aspect of larva and cephalic

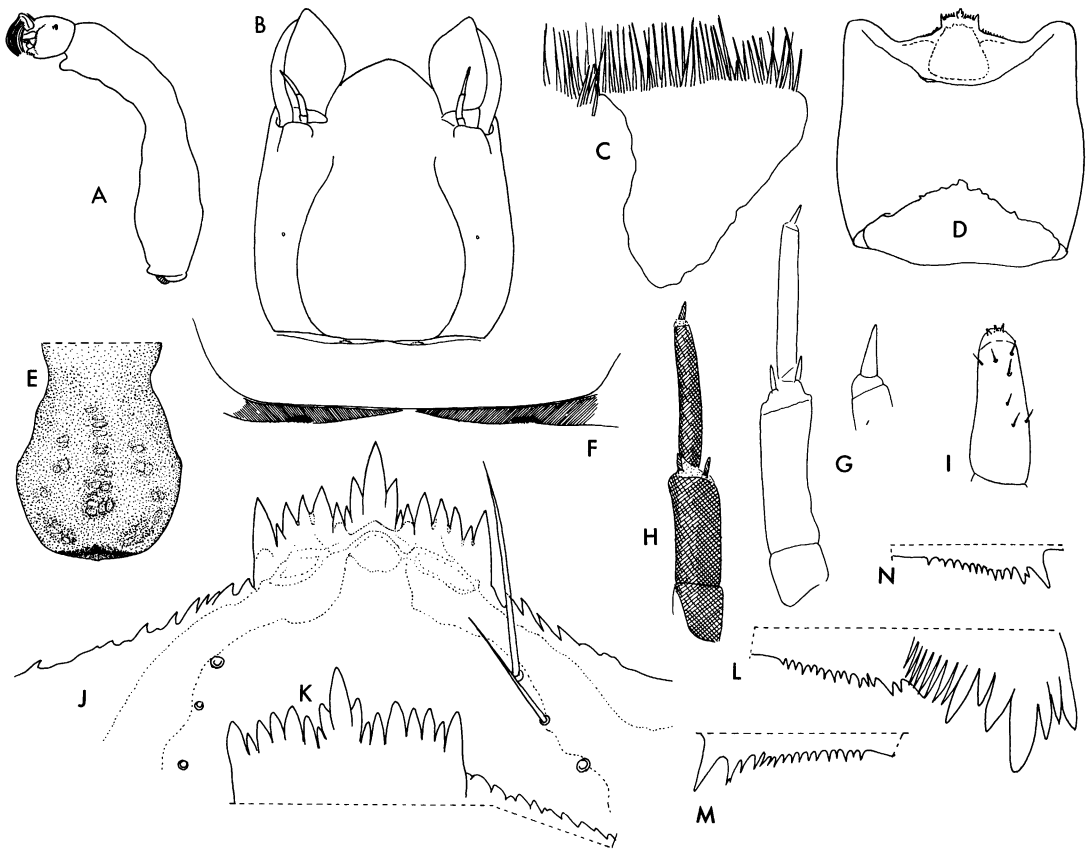

Fig. 16. *G. carmenae.* Larva. **A.** Larva, side view. **B.** Head, dorsal view. **C.** Lateral sclerite of foreleg. **D.** Cephalic capsule from below. **E.** Cephalic apotome. **F.** Cervical sclerites. **G.** Antenna with apical sensillum. **H.** Antenna. **I.** Maxillary palp. **J.** Hypostomium. **K.** Portion of different hypostomium. **L.** Apex of mandible. **M, N.** Mandibular serrations.

apotome as shown in figure 16A, E. Antenna shorter than width of base of mouthfans (fig. 16B); second article more than two times as long as basal article and approximately equal to the length of third article (fig. 16G, H). Apical sensillum 2.5 times as long as wide at base. Mandible (fig. 16L–N) with 11–12 inner teeth and numerous marginal serrations (15–16). Maxillary palp (fig. 16I) three times as long as wide at base. Ventral aspect of cephalic capsule as in figure 16D. Hypostomium as illustrated in figure 16J, K. Median tooth surpassing level of apex of corner teeth. Line connecting apex of median tooth to apex of fourth lateral tooth not intersecting corner tooth. Each side of sclerite with three hypostomial setae and 8–10 lateral serrations. Cervical sclerites (fig. 16F) narrow, pointed mesially, their points approaching very closely. Lateral schlerite of proleg with about 50 teeth (fig. 16C).Perianal scales not observed. Crochet ring composed of approximately 105 rows of 16–20 hooks each. Anal gills not examined.

HOLOTYPE: ARGENTINA: *Rio Negro:* Arroyo La Cascada, Cerro Catedral, Feb. 14, 1967 (S. Coscarón; MLP), 1 pupa with pharate male.

ADDITIONAL SPECIMENS: Two larvae, same data as holotype.

ETYMOLOGY: The species is named for Carmen Coscarón, wife of the senior author, who helped with fieldwork in southern South America.

BIOLOGY: Pupa and larvae were collected on stones in a creek with a torrential current and cold, crystalline waters.

DISCUSSION: This peculiar species is very close to *G. igniculus.* Unfortunately we had few specimens, but the pupal gill permits dif-

ferentiation from all other species of *Gigantodax*. Minor differences, as shown in the key, allow separations from *igniculus*.

Gigantodax igniculus
Coscarón and Wygodzinsky
Figures 17A–R, 18A–K, 19A–G, 20A–L, 21A–D, 22A–L, 178A

Gigantodax igniculum Coscarón and Wygodzinsky, 1962: 296. Vulcano, 1967: 3; 1977: 290. [Incorrect gender.]

DIAGNOSIS: *Gigantodax igniculus* is characterized by the virtual absence of spinules on R_1, the short calcipala not extending beyond the basal third of the second tarsomere, the hooklike processes of the claws of the female, the heavily spined aedeagus, the large number of respiratory filaments of the arborescent respiratory organ of the pupa, and the very short basal segment of the antenna of the larva.

REDESCRIPTION: *Female.* Length of wing 3.4–3.9 mm. Head, and to a lesser degree, mouthparts dark brown. Clypeus, with abundant silvery pilosity. Vertex and posterior margin of eyes with silvery setae. Antenna dark brown, with scapus and pedicellus slightly lighter. Scutum orange colored, with somewhat darker area as shown in figure 17C. Scutum covered with silvery to reddish decumbent pilosity. Scutellum and metanotum light reddish-brown, metanotum with silvery pruinosity. Pleura brown, with a tuft of brown setae. Halter pale gray. Wing translucent. Veins pale brown; hairs and spinules black. Legs (fig. 17J, K) light brown, their setae appearing light brown, silvery or black. Pigment distribution difficult to make out, best observed in slide mounts. Abdominal hairs, including basal fringe, from silvery to brown.

Frontal angle approximately 90° (fig. 17A). Fronto-ocular triangle (fig. 17B) as wide as high. Shape and proportions of antennal segments as shown in figure 17D. Mandible (fig. 17E) with teeth only at inner edge, their number 12–16. Maxilla each with approximately 22 teeth. Distal segment of maxillary palp two-thirds as long as penultimate (fig. 17G). Second segment of maxillary palp suboval (fig. 17H), twice as long as wide. Sensory vesicle (fig. 17I) oval, without neck, about one-fourth as long as second segment of maxillary palp. Sc with 35–43 hairs. R_1 with two or three rows of irregularly arranged setae. Setae on R_s in two rows. A_1 almost attaining wing margin. Hind basitarsus 6.7–7.0 times as long as wide. Calcipala only attaining level of basal third of second tarsomere (fig. 17L). Basal tooth of claw (figs. 17M, 178A) pointed, slightly curved, as heavily sclerotized as remainder of claw. Eighth abdominal sterna with delicate hairs only (fig. 17N, O). Gonapophyses well sclerotized on the internal border and projected directly. Cercus subovoidal and paraproct short (fig. 17N–P), genital fork as figure 17Q, and spermatheca subglobose (fig. 17N, R).

Male. Color as in female, but light-colored areas with more saturated color, and dark elements of scutum in many cases with dark color coalesced into narrow black stripe along midline. Holoptic. Length of wings 3.3 mm. Shape and proportions of antennal segments similar to those of female, viz., first flagellomere not longer than wide. Distal segment of maxillary palp slightly longer than penultimate (fig. 18A, B). Sensory vesicle (fig. 18C) small, subglobose, with distinct neck. Sc with 30–38 hairs; remainder of wing as in female. Shape and proportions of fore and hind leg segments shown in figure 18D, E. Fore basitarsus nine times, hind basitarsus 4.7 times as long as wide (fig. 18F). Calcipala covering only extreme base of second tarsomere (fig. 18G). Genitalia of male as illustrated (figs. 18H–K, 19A–G), characterized by the apically emarginate ventral plate, by the well sclerotized large basal arms of the ventral plate and by the large number of spinules on the aedeagal membrane. Endoparameral organ normally developed.

Pupa. Cocoon formed by an irregular, dense fabric, its color light brown. Cocoon covering body of pupa to near insertion of gills (fig. 20A, B). Body of pupa dark brown, darkest in cephalic and distal region.

Gills perpendicular to longitudinal axis of body of pupa, not over 2.5 mm in length, light brown, arborescent, with 90–120 terminal branches (fig. 20A–E). Gills shortly pedunculate at base, divided into four main branches, with large number of secondary and tertiary branches, the latter filamentous. Apex of filaments rounded. Frontoclypeus of female and male pupae as shown in figure 20H–K. Only facial trichomes present, short, spiniform (fig. 20G). Frontoclypeus and thorax

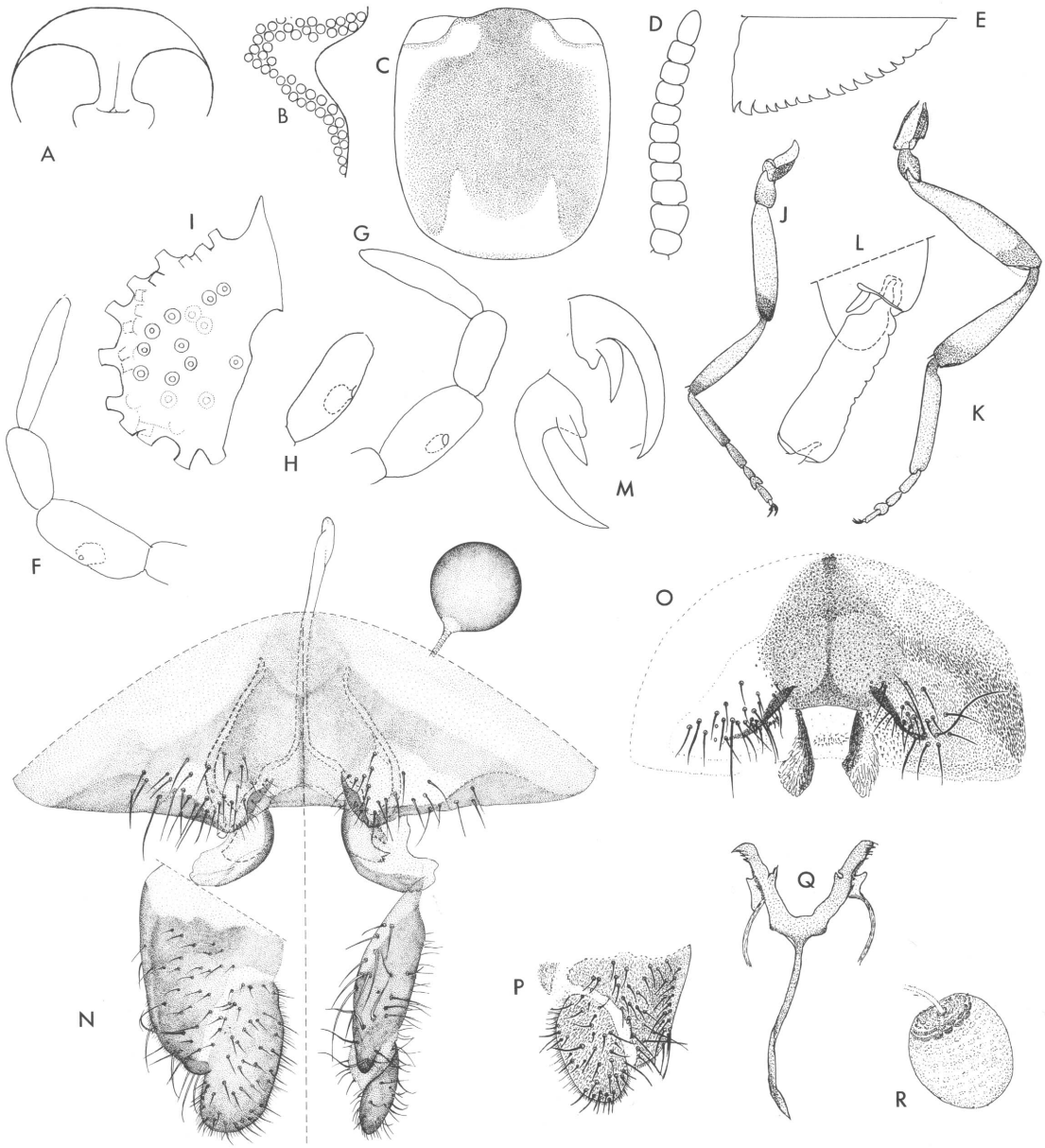

Fig. 17. *Gigantodax igniculus.* Female. **A.** Frons and vertex. **B.** Fronto-ocular triangle. **C.** Scutum. **D.** Antenna. **E.** Apex of mandible. **F, G.** Maxillary palp. **H.** Second article of maxillary palp. **I.** Sensory vesicle of maxillary palp. **J.** Median leg. **K.** Hind leg. **L.** Calcipala, with second tarsal segment. **M.** Claws of different specimens, in slightly different views. **N.** Genitalia in normal position (left cercus and paraproct mounted on slide). **O.** Eighth sternite, with gonapophyses. **P.** Cercus and paraproct. **Q.** Genital fork. **R.** Spermatheca.

with numerous irregularly distributed smooth platelets (fig. 20L). Dorsolateral trichomes of thorax slender, the dorsocentral one thickest (fig. 21A). Setae of abdominal tergite I very short, hairlike, length 20 mm; those of abdominal tergite II spinelike, length 10–15 mm (fig. 21C). Setae of tergites III–VIII short and slender, length on tergite VII 20–25 μm.

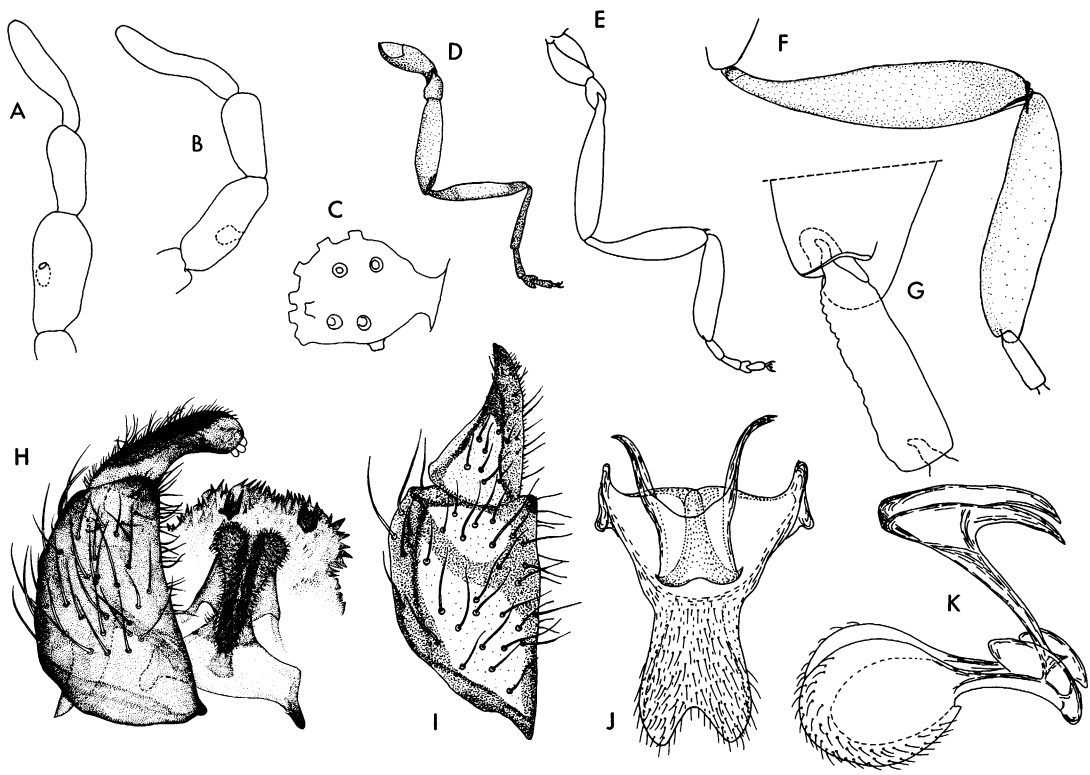

Fig. 18. *G. igniculus.* Male. **A, B.** Maxillary palps. **C.** Sensory vesicle of maxillary palp. **D.** Foreleg. **E.** Hind leg. **F.** Tibia and basitarsus of hind leg. **G.** Calcipala with second tarsal segment. **H.** Genitalia in normal position. **I.** Basimere and distimere. **J.** Median sclerite with ventral plate. **K.** Ventral plate with median sclerite, side view.

Spinecombs on tergites VI–VIII, variously interrupted, on tergite VII consisting of 30–36 spines, length about 10 μm. Setae of tergite VIII simple or bifurcate. Tergites III and IV each with 4 + 4 short hooks. Tergites VI–VIII with spine-combs, on tergites VI and VII each with 30–35 teeth. Spine-combs of tergite VIII consisting of 40–42 teeth. Sternite V with 3 + 3, VI with 2 + 2, and VII with 1 + 1 hooks. Sternites VI and VII divided along middle by distinct membrane. Some spine-like setae also in intersegmental membranes (fig. 21B–D).

Mature larva. Length 6–7 mm. Maximum width of head 7 mm. General body shape as in *carmenae.* Larva greenish brown, distal segments dark brown. Head dark brown. Cephalic apotome lighter, with dark spots (fig. 22A). Cephalic apotome widest at some distance from base of sclerite. Hypostomial bridge as shown in figure 22B. Antenna darkly pigmented (fig. 22C), pigment most intense on distal segments. Antenna very short, extending only to level of middle of stems of cephalic fans. Ratio of length of antennal segments I–III = 1:2.3–2.6:2.6–3.4, viz., first segment unusually short. Terminal sensillum of antenna 5 times as long as wide at base. Cephalic fan with 23–25 large rays. Mandible with 9 inner teeth and approximately 22–30 marginal serrations (fig. 22D). Maxillary palp as in figure 22E. Hypostomium as shown in figure 22F, G. Median tooth slightly surpassing level of apices of corner teeth. Line connecting apex of fourth lateral to apex of corner teeth meeting at obtuse angle. Hypostomium with three to six lateral serrations and four to six hypostomial setae. Cervical sclerites as in *carmenae,* with their internal extremes approaching very closely. Histoblast of pupal gill conspicuous. Proleg sclerite with 46–52 teeth disposed in one to three

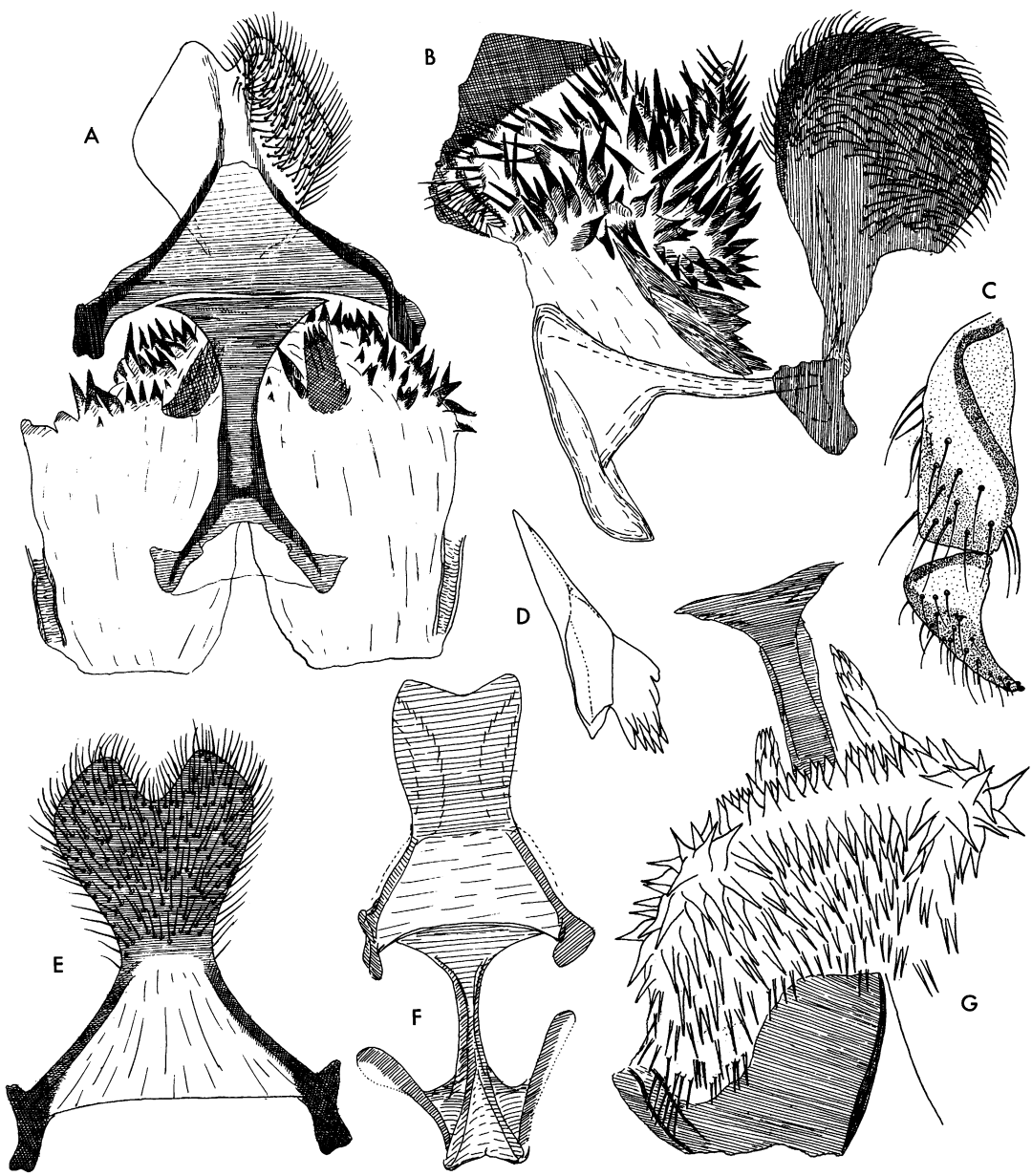

Fig. 19. *G. igniculus.* Male. **A.** Ventral plate, median sclerite, endoparameral organ, and aedeagus, seen from below. **B.** Same, side view. **C.** Basimere and distimere. **D.** Portion of endoparameral organ. **E.** Ventral plate. **F.** Ventral plate and median sclerite. **G.** Portion of aedeagus.

rows, shape as in *carmenae.* Perianal scales well developed, forming complete perianal ring (fig. 22H). Recurrent struts not well developed. Crochet ring with about 125–190 rows composed of 22–40 hooks each.

First instar larva as illustrated in side view (fig. 22I), egg tooth and oval cephalic apotome shown in figure 22J. Aspect of eggs as shown in figure 22K, L.

MATERIAL EXAMINED: ARGENTINA: *Tierra del Fuego:* Ushuaia, Feb. 10, 1967 (A. Bachmann; INM), several larvae; Puerto Al-

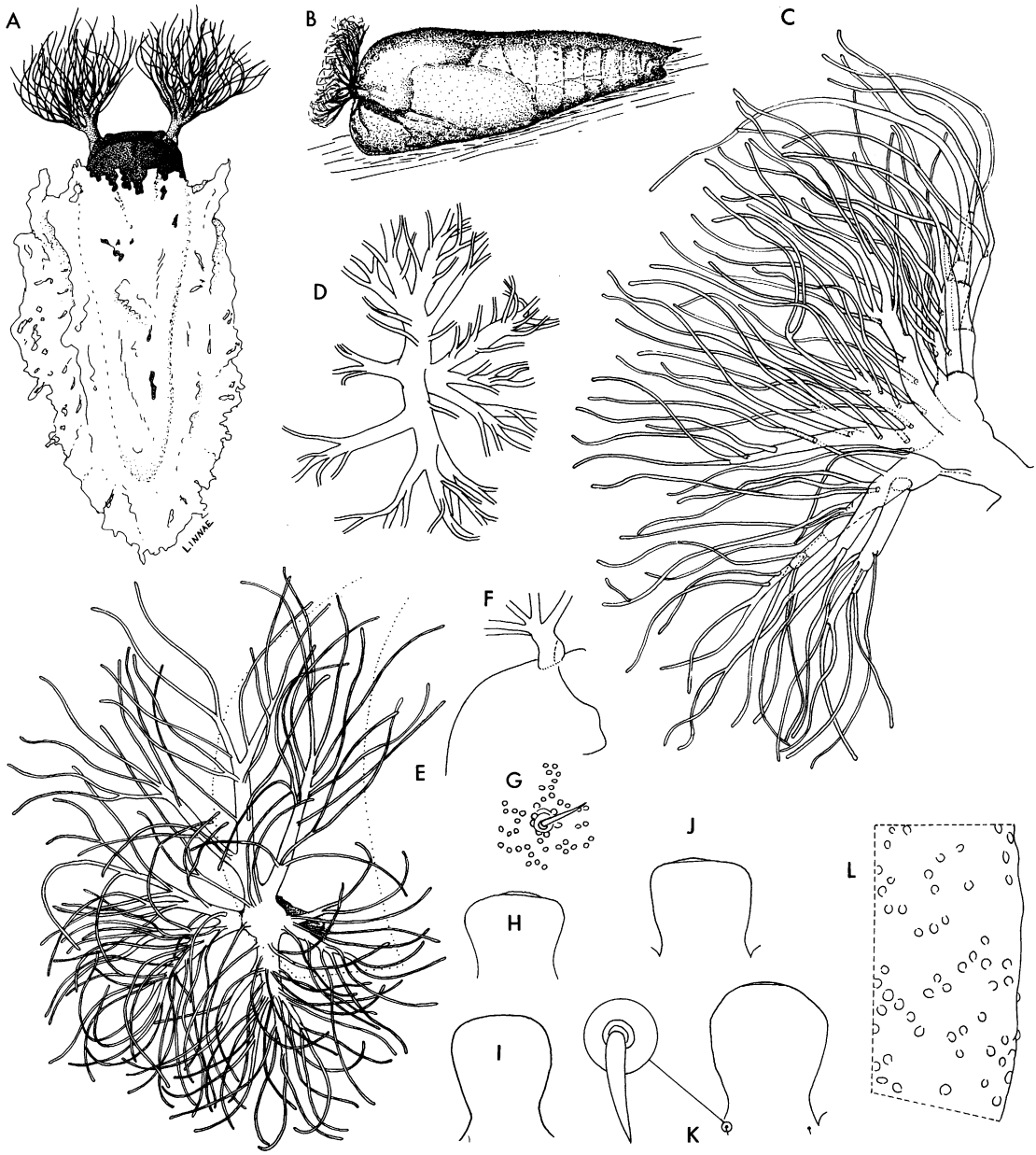

Fig. 20. *G. igniculus.* Pupa. **A.** Pupa in cocoon, dorsal surface. **B.** Same, side view. **C.** Gill. **D.** Base of gill, spread out. **E.** Gill in different view. **F.** Base of gill of other specimen. **G.** Trichome at base of frontoclypeus. **H, J.** Frontoclypeus of female. **I, K.** Same, male. **L.** Platelets of thorax. All specimens from Tierra del Fuego, except A, F, and L, which are from Cerro Catedral.

manza, Oct. 15, 1953 (M. Garcia; MLP), larvae; Isla de los Estados [Staten Island], Arroyo Cook, Nov. 26, 1967 (A. Bachmann; INM), larvae. *Santa Cruz:* Lago Argentino, March 8, 1953 (A. Willink, IML), 1 male; IML, *Rio Negro:* Bariloche, Arroyo Lopez, Jan. 14, 1967 (S. Coscarón; AMNH), several larvae and pupae; Cerro Catedral, 1800 m,

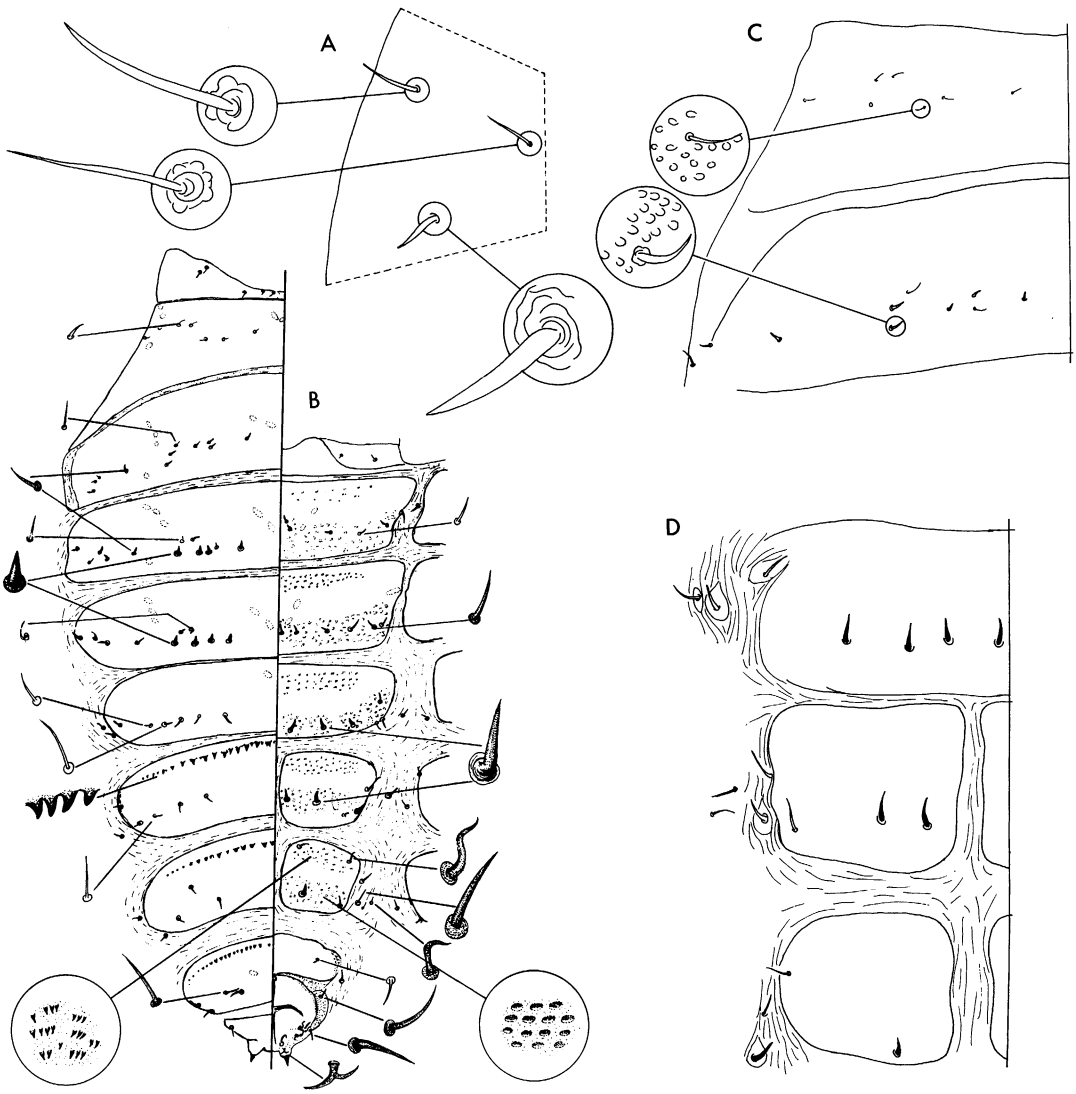

Fig. 21. *G. igniculus.* Pupa. **A.** Trichomes of thorax. **B.** Chaetotaxy of abdomen. **C.** Chaetotaxy of abdominal tergites I and II. **D.** Tergites V–VII.

Feb. 14, 1967 (S. Coscarón; AMNH), larvae and pupae, 2 males, 2 females (reared with pupal exuviae); same, Feb. 16, 1973 (S. Coscarón; MLP), larvae and pupae; same Oct. 27, 1975, larvae; same Feb. 2, 1977 (S. Coscarón; MLP), larvae and pupae; same Jan. 18, 1983 (S. Coscarón; MLP), larvae and pupae; same April 10, 1983 (S. Coscarón; MLP), larvae and pupae. Arroyo de la Cascada, base of Cerro Catedral, Jan. 22, 1971 (S. Coscarón; MLP), 1 larva. *Neuquen:* Arroyo Huemul, N of Brazo Huemul, Lake Nahuel Huapi, Feb. 15, 1967 (S. Coscarón; AMNH), larvae. San Martin de los Andes, Cerro Chapelco, 1600 m, Jan. 30, 1979 (S. Coscarón; MLP), pupae and larvae. CHILE: *Magallanes:* Isla Deceit, Nov. 27/Dec. 3, 1982 (D. Lanfranco; MLP), 1 female. *Aysen:* Puerto Cristal, Lago Buenos Aires, Sept.–Oct., 1959 (L. Pena; CNC), 1 female. *Malleco:* Curacautin, Dec. 19, 1950 (L. Pena; CNC), 1 female. *Nuble:* 40 km E of San Carlos, Dec. 24, 1950

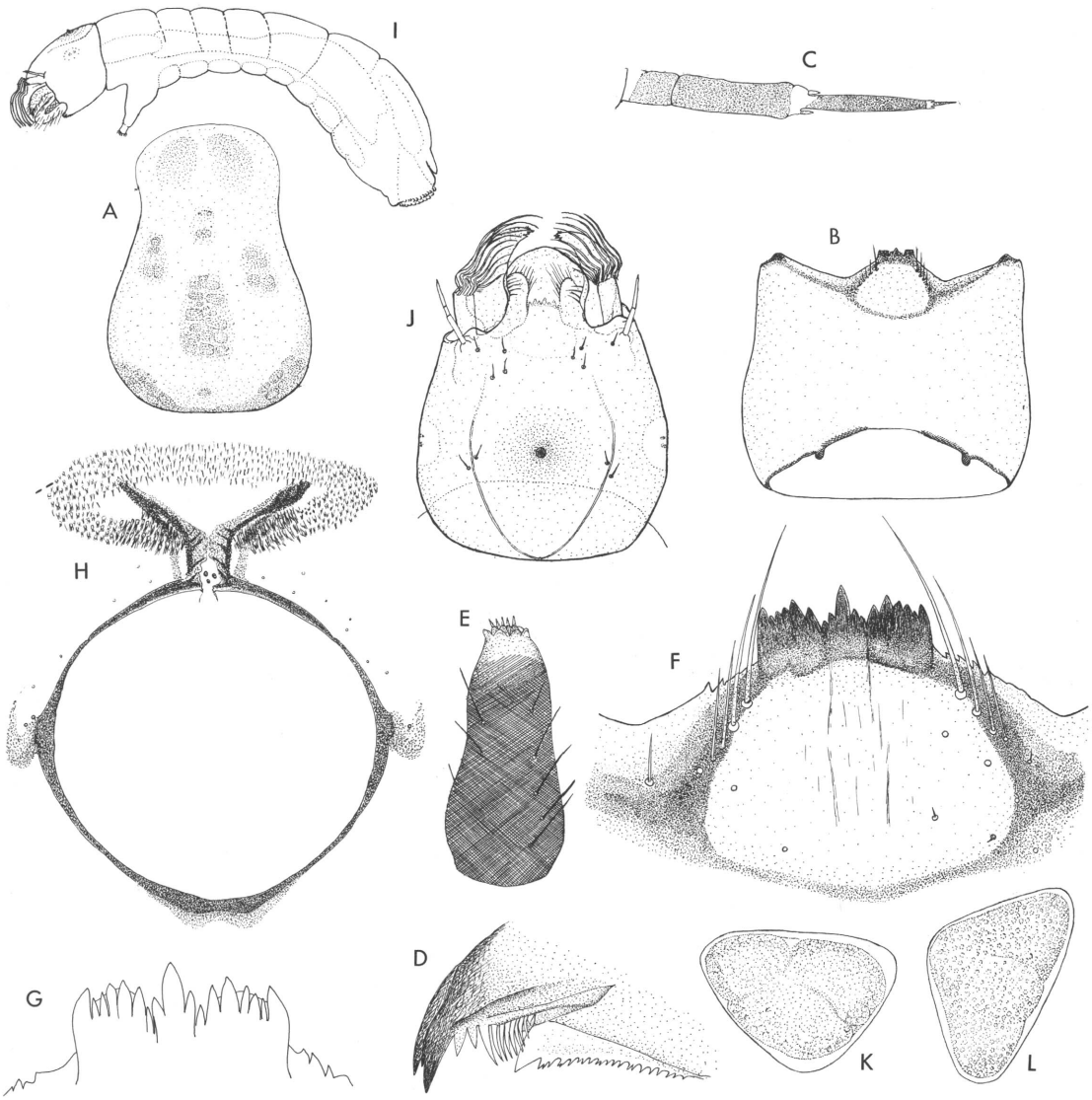

Fig. 22. *G. igniculus.* Larva. **A.** Cephalic apotome. **B.** Cephalic capsule, under surface of head. **C.** Prepupal larva: Antenna. **D.** Apex of mandible. **E.** Maxillary palp. **F.** Hypostomium. **G.** Anterior portion of hypostomium. **H.** Anal sclerite. **I.** First instar, side view. **J.** Head of first instar larva, dorsal view. **K, L.** Eggs.

(E. Ross and A. Michelbacher; CAS), 2 females. *Curico:* Fundo La Montana, Estero La Palma, Rio Teno, 6 km E of Los Quenes, Jan. 4, 1967 (Irwin and E. Schlinger; CIS), 1 female.

DISCUSSION: *G. igniculus* has peculiar characters in the female and male genitalia, pupal gill, proportions of the antennal segments and the cephalic apotome in larvae that distinguish it from other species. It is closest to *carmenae,* but the shape of the pupal gill permits separation of the two species.

minor group

DIAGNOSIS: Species of this group are recognized by the small size and weakly sclerotized preimaginal stages, the presence of the hook-shaped subbasal claw tooth, a mandible

with teeth on both sides, comparatively large spermatheca in females; spinules on aedeagus, the apically hooked trichomes of frontoclypeus and thorax, filamentous branches not over 13 on pupal gill, and elongated larval antenna with very short second segment, and very elongate third segment with a terminal sensillum.

FEMALE: Coloration from orange to brownish blackish. Frons, eye, antenna, and maxillary palp normal. Sensorial organ of maxillary palp comparatively poorly developed (figs. 23F, G, 27D, F). Mandible with teeth on both sides (figs. 23C, D, 27C). Scutum with only recumbent hairs. Wing spinules ranging from absent to well developed on R_1 (fig. 23I, J). Calcipala well developed, extended distinctly past the middle of second tarsomere (figs. 23O, 27I, 31F). Subbasal tooth of claw hook-shaped (figs. 23P, 27J, K, 31G–I, 178B). Lateral arms of genital fork wide and parallel (figs. 23R–T, 27M, 31M). Spermatheca well sclerotized and large (figs. 23R, 31K). Gonapophyses slightly projected distally and with several setae (figs. 23R, 27L, 31K).

MALE: Color as in female or a little darker. Holoptic, without fronto-ocular triangle. Mesonotum gibbous. Ventral plate with distal concavity (figs. 24N, 28L, M). Aedeagus with small spinules (fig. 24P).

PUPA: Cocoon very poorly developed. Gill with 11–13 filamentous branches (figs. 25A, B, 26A, B, 29A–E). Frontoclypeus with facial and obsolescent frontal trichomes. Trichomes of frontoclypeus and thorax hooked distally (figs. 26C–E, 29G, H). Abdominal tergite I with trichomes reduced (1 + 1 till 3 + 3). Terminal hooks elongated, pointed (figs. 25H, 26F); setae of segments VIII–IX simple.

LARVA: Body cuticle without hairs. Cephalic apotome widest near base (fig. 30A–C). Antenna longer than stem of cephalic fans; second segment shorter than one-half length of basal segment, third longer than basal plus second segments (figs. 26H, 30D, E), terminal sensillum ratio length/width over 6 (figs. 26I, 30F). Marginal serrations of mandible reduced (figs. 26J, 30H, I). Hypostomium with medium tooth at same level or below the corner teeth (figs. 26M, N, 30K, L). Recurrent struts not perceptible or weakly developed (fig. 26P). Anal scales not forming a complete circumanal ring. Anal gill with three single lobes.

DISTRIBUTION: Patagonian Andes, central and northern Chile, and Bolivia (fig. 32).

DISCUSSION: The *minor* group has in common with the *multifilis, wrighti,* and *igniculus* species groups two apomorphies: mesonotum gibbous, especially in the males, and a second antennal article no longer than the first. Also, the *minor* group has several characters that easily permit differentiation from other groups: in the female, a mandible with teeth on both sides (unique presence in *Gigantodax,* but it is common with some other Neotropical Prosimuliini, such as *Mayacnephia, Araucnephioides, Cnesiamima,* and *Paraustrosimulium*—probably a consequence of parallelism) and an enlarged spermatheca. In the pupa, trichomes of the frontoclypeus and thorax are apically hooked and setae of abdominal tergite I are reduced to 1 + 1 or 3 + 3; in the larva the antenna is thin and elongated with the third article longer than first and second character combined; the terminal antennal sensillum is very long (the last character in common with *multifilis* group and the lower species of *wrighti* group); and there is a reduced number of marginal serrations on the mandible, great reduction of the recurrent struts, and anal scales that do not form a complete circumanal ring in the larvae.

The *minor* group also shares three synapomorphies with the *igniculus* group as was mentioned previously.

Four species are included in this group: only *minor* is known completely. In *araucanius* the larva is unknown, and in *eremicus* only the larva and pupa are known. *Gigantodax bolivianus,* known only from females, is tentatively included here although it is incompletely known.

Gigantodax araucanius (Edwards)

Figures 23A–T, 24A–P, 25A–H

Simulium (*Gigantodax*) *araucanium:* Edwards, 1931: 142. Orfila, 1935: 1529. Vargas and Diaz Najera, 1951a: 155.

Gigantodax araucanium: Wygodzinsky, 1961a: 460; 1961b: 563. Vulcano, 1967: 3; 1977: 290. [Incorrect gender.]

DIAGNOSIS: Blackish species with calcipala almost attaining the extremity of the second

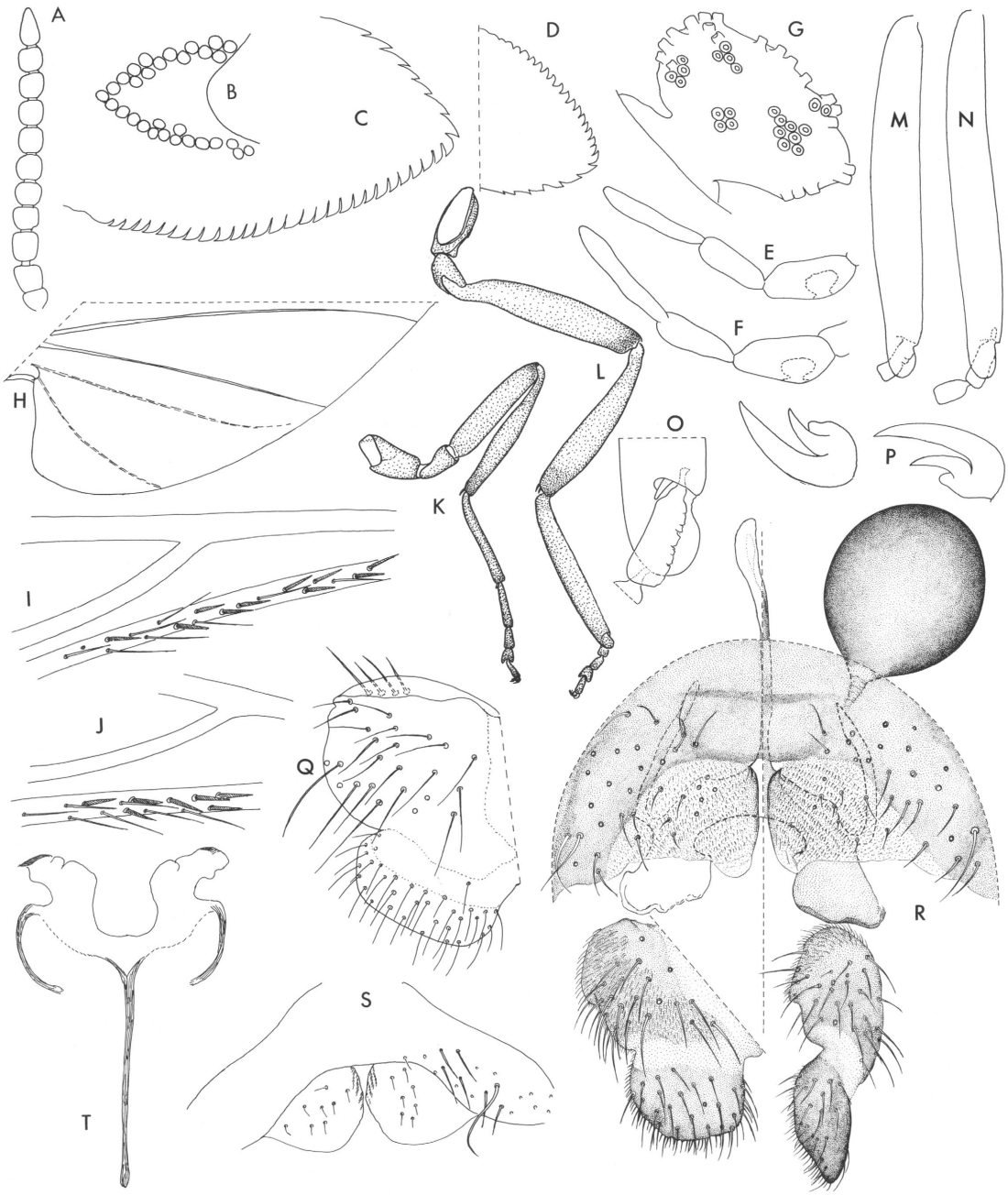

Fig. 23. *Gigantodax araucanius.* Female. **A.** Antenna. **B.** Fronto-ocular triangle. **C.** Apex of mandible (Dalcahue). **D.** Same (Ancud). **E.** Maxillary palp (Ancud). **F.** Same (Dalcahue). **G.** Sensory vesicle of maxillary palp. **H.** Portion of wing. **I.** Portion of R_1 (Ancud). **J.** Same (Lago Frio). **K, L.** Fore and hind legs. **M, N.** Hind basitarsus with second tarsal article. **O.** Calcipala. **P.** Claws in different position. **Q.** Cercus and paraproct. **R.** Genitalia in normal position; cercus and paraproct on left side on slide position. **S.** Gonapophyses. **T.** Genital fork.

tarsomere, claw with subbasal teeth hook-shaped, pointed; pupal gill with 11 filaments arising from a short basal trunk, and sparse platelets on head and thorax.

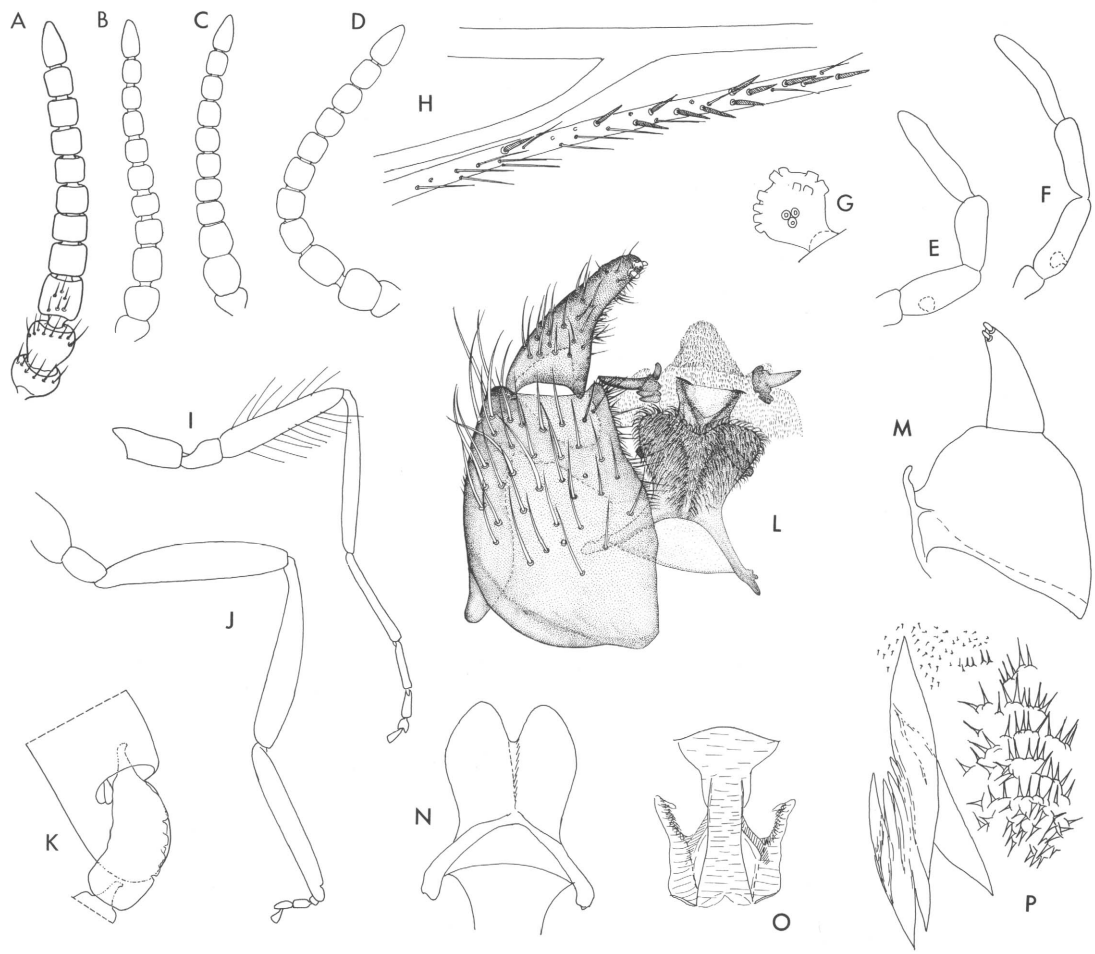

Fig. 24. *G. araucanius.* Male. **A–D.** Antennae (B is paratype from Chiloe). **E.** Maxillary palp (Dalcahue). **F.** Same (Paratype from Chiloe). **G.** Sensory vesicle. **H.** Portion of R_1 (Paratype Ancud). **I, J.** Fore and hind legs. **K.** Calcipala. **L.** Genitalia in normal position. **M.** Basimere and distimere. **N.** Ventral plate. **O.** Median sclerite. **P.** Endoparameral organ with spinules of aedeagus.

REDESCRIPTION: *Female.* Length of wing 3.0–3.8 mm. Head blackish. Eye, frons, occiput, clypeus, antenna, and maxillary palp dark castaneous; frons and clypeus with gray polinosity; antenna with very delicate and short pilosity, flagellum silver gray, scapus and pedicelus with hairs longer and scattered, appearing to be more lightly colored than the remainder. Setae of frons, occiput, clypeus, and maxillary palp dark brown. Thorax dark brown with scutum from black to dark grayish castaneous, with lateral and pronotal borders brown. Setae situated on black part of scutum, copper brown or bronze according to light, those of lateral areas lighter; scutellum reddish castaneous with lateral setae more clear colored. Grayish pilosity. Pleura from blackish brown with setae of black color and metanotum from dark brown to black with grayish pollinosity. Legs from brownish yellow to blackish brown with articulations and tarsi with brownish yellow to black setae. Wings translucent, with brown veins, setae with spines dark brown. Halter light brown. Abdomen dark brown, somewhat lighter colored ventrally. First abdominal tergum with large rust colored setae, the remaining black.

Frons with short median sulcus. Frontoocular triangle slightly longer than wide (fig. 23B). Shape and proportions of the antennal articles as in figure 23A. Mandible generally with teeth on both sides (fig. 23C, D). Max-

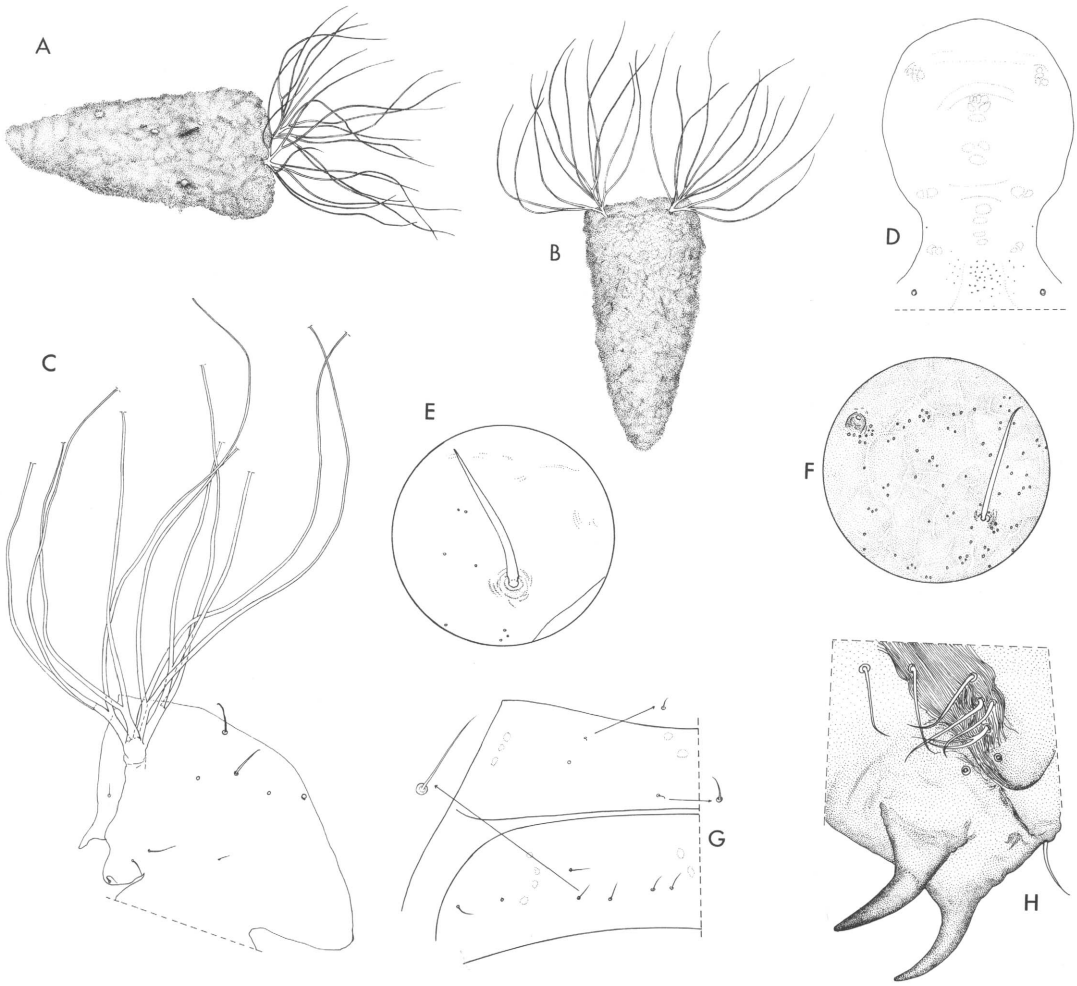

Fig. 25. *G. araucanius.* Pupa. **A, B.** Pupa in lateral and dorsal view. **C.** Gill branches and trichomes of thorax. **D.** Frontoclypeus of male. **E.** Detail of frontoclypeus trichome. **F.** Detail of thorax trichome. **G.** Chaetotaxy of abdominal tergites I and II. **H.** Distal portion of abdomen.

illiary palp and sensorial vesicle as shown in figure 23E, F and 23G respectively; maxilla with 26 to 30 teeth. Wings as with A_1 showing small curvature (fig. 23H), R_1 with numerous spinules or spiniform setae from discal curvature of Sc arranged in one or two files, frequently more abundant than the setae (fig. 23I, J). Shape, proportions, and distribution of pigment of fore and hind legs as in figure 23K, L. Pigmentation of legs variable from almost totally pigmented to pigment only on articulations and tarsi. Shape of hind basitarsus as in figure 23M, N, ratio length/width = 8. Calcipala longer than wide (fig. 23O). Claw as in figure 23P. Genetalia as shown in figure 23Q–T. Sternite VIII distinctly pigmented and with 20 to 25 setae on each side; cercus flattened.

Male. Wing length 3.0–3.8 mm. Head and appendices black with hairs concolorous. Thorax black with pronotal and pleural areas sometimes dark brown. Legs dark brown with hairs from brown to black. Wings as in female. Halteres dark brown. Abdomen black with ventral area lighter. Setae of first abdominal segment from light brown to black according to light. Remaining setae black.

Shape and proportion of antenna as shown

in figure 24A–D. Maxillary palp as figure 24E, F. Sensorial vesicle with short neck (fig. 24G). Setae of scutum and scutellum as in female, as are also the wings. Shape and proportion of articles of fore and hind legs as figure 24I, J. Setae of Rs as figure 24H. Calcipala (fig. 24K) longer than wide and almost as wide as the second posterior basitarsus. Ratio length to width of basitarsus 1:7.5. Genitalia as shown in figure 24L–P, with internal hooks at end of parameres short. Median sclerite as shown in figure 24O.

Pupa. Cocoon covering entire body leaving free only the gills (fig. 25A, B). Cocoon light brown, thick, with irregular texture mesh perceptible, outline of pupa not visible through cocoon.

Length of body of pupa about 4.0–5.0 mm, cephaloptherotecal distance 2.7–2.8 mm. Length of gill filaments 2.8–3.2 mm, their color dark grayish brown. Eleven filaments arranged in arborescent shape, with four short primary branches arising from a short basal trunk (fig. 25A–C); filaments relatively thin and gradually narrowing towards apex. Head and thorax light colored, polished, with very scarce platelets (fig. 25D). Frontoclypeal shape and trichomes as in figure 25D, E, with 1 + 1 big facial and 1 + 1 small frontal trichomes. Thorax with three big dorsocentral trichomes and 3–6 smaller ones situated on exposed portion (fig. 25C, F). Setae of abdominal tergites I and II hairlike (fig. 25G). Tergites III–IV each with 4 + 4 hooks; anterodorsal setae spinelike; spine-combs on tergites VI–VIII continuous with 26–48 spines. Specialized setae of segment VIII–IX variously bent, some of them biramous (fig. 25H). Sternite IV with 4 + 4, V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooklike setae; pleural membrane with one hook on segments VI and VII. Terminal hooks elongated.

Larva. Unknown.

BIOLOGY: This species breeds in small streams on stones and aquatic plants. It was collected together with *G. minor, G. marginalis,* and *G. fulvescens.*

MATERIAL EXAMINED: ARGENTINA: Isla de los Estados, Puerto Basil Hall, 20–23 May, 1971 (Flint; USNM), 1 female; Bahia Crossley, Apr. 26–30, 1971 (Flint; USNM), 1 female; Bahia York, Puerto Rico Celular, May 4–6, 1971 (Flint; USNM), 1 female. *Rio Negro:* Bariloche, Jan. 26, 1983 (S. Coscarón; MLP), 2 pharate females, 1 pharate male, pupae. CHILE: *Magallanes:* Isla Deceit, Nov. 27–Dec. 3, 1983 (Lanfranco, D; MLP), 11 females, 4 males. *Aysen:* Lago Frio, Coihaique, Valley of Rio Simpson, Jan. 20–23, 1961 (L. Pena, CNC), 27 females; Coihaique, 1150 m, Feb. 10, 1936 (Kuschel; MHN), 1 female; Puerto Cisnes, Feb. 1–15, 1961 (L. Pena, CNC), 1 female; *Chiloe:* Mechuque, Dec. 23, 1926 (F. and M. Edwards; AMNH), paratype female; Dalcahue, Jan. 17–22, 1962 (L. Pena, CNC), 63 females; same, Jan. 17–31, 1962 (CNC), 4 females, 1 male; same, Feb. 1–8, 1962, 1 female, 2 males; same, March 1–4, 1962, 1 female; Melinka, Arch de los Chonos, Jan. 28–31, 1962 (L. Pena; CNC), 1 female. *Llanquihue:* Puerto Varas, Dec. 16, 1926 (F. and M. Edwards; AMNH), 1 paratype female. *Osorno:* 10 km N of Puyehue (Ross and Michelbacher; CAS), 1 female.

DISCUSSION: This species is dark in well preserved specimens, making it easy to distinguish from the remaining *Gigantodax* species of the area. Although dark forms of *chilensis* or *marginalis* can cause doubts, the hook-shaped claws permit differentiation of the females. The presence of a great number of spines on R_1, which begin before the distal curvature of Sc and in more than one row, is useful for identification. Another distinguishing character is the presence in the female of a proportionally large spermatheca, and in the male, larger spines on the membrane of the aedeagus. The pupal gill with 11 branches (as in *minor*) permits differentiation from other species; the very short stem gill is useful for separating *araucanius* from *minor.*

By its color, *araucanius* could be confused with *Araucnephioides schlingeri* (Wygodzinsky and Coscarón), *Cnesiamima antroparva* (Edwards), *Paraustrosimulium anthracinum* (Bigot). It is distinguished from the first and second, which have a straight Cu, and from the third by the presence of 11 antennal segments.

Our material agrees well with the paratypes of Edwards deposited in the AMNH and USNM, as well as with the original description. We have also examined the holotype and several paratypes in the BM; our specimens agree with that material.

Gigantodax eremicus, new species
Figure 26A–P

DIAGNOSIS: A species distinguished from all congenerics (except *minor*) by the extremely short second segment of the antenna of the larva. *Gigantodax eremicus* can be distinguished from *G. minor* by the median tooth of the hypostomium reaching the level of the corner teeth, and by the 13 gill branches.

DESCRIPTION: Female and male not known.

Pupa. General aspect as in *minor.* Color of cocoon light brown, consisting of irregularly arranged loose threads covering abdomen and parts of thorax of pupa. Length of gills approximately 2 mm, their general aspect shown in figure 26A, B; gills much as in *G. minor,* but with 13 flexible, slender branches inserted on 3 primary branches, the latter inserted close to each other on elongate trunk about five times as long as wide. Frontoclypeus of female pupa with few and smooth platelets (fig. 26C), with trichomes short and slender, hooked apically. Thorax with dorsocentral trichomes hairlike, dorsolateral trichomes stronger, hooked apically (fig. 26A, D, E). Abdomen poorly preserved, and not studied in detail. Specialized setae of segments VIII and IX long, simple. Terminal spines of abdomen elongate, pointed (fig. 26F).

Mature larva. Maximum length observed 6.5 mm. Shape as shown in figure 26G. Color dark brown, head lighter; positive spots on cephalic apotome faintly marked. Antenna (fig. 26H) slightly longer than stem of cephalic fan; ratio of segments I–III = 1:0.3:1.5. Terminal sensillum (fig. 26I) about 6.5 times as long as wide at base. Cephalic fan with approximately 38 large rays. Apex of mandibles (fig. 26J, K) similar to that of *minor,* with eight to nine inner teeth, and two to three marginal serrations. Maxillary palp (fig. 26L) slender, almost three times as long as wide. Hypostomium (fig. 29M, N) with apical and median teeth at, or very close to, level of apex of corner teeth. Imaginary line connecting apex of median tooth to apex of fourth lateral tooth intersecting several other teeth. Line connecting apices of fourth lateral teeth to apices of corner teeth forming angle of 80°. Hypostomium with two to three hypostomial setae and two to three lateral serrations. Cervical sclerites in shape of narrow transverse bands, capitate at inner extremities (fig. 26O). Perianal region as shown in figure 26P. Perianal setae simple. Recurrent struts weakly developed. Crochet ring with 80–90 rows composed each of 14–15 hooks.

HOLOTYPE: CHILE: *Atacama:* Quebrada de San Andres, 2400–2600 m, Oct. 20–26, 1967 (S. Coscarón; AMNH), pupa.

ADDITIONAL SPECIMENS: Same data as holotype, 1 larva (AMNH). CHILE: *Atacama:* 10 km W of San Andres, 1900 m, Oct. 26, 1967 (S. Coscarón; AMNH), 3 larvae.

ETYMOLOGY: From the greek *eremos,* solitary, lonely.

BIOLOGY: The three larvae collected at 1900 m were found on stones; the larvae collected between 2400 and 2600 m were adhering to leaves of *Potamogeton* sp. The water in the streams was brackish with salt crystallizing at the shore. Water temperature was 17°. The aquatic fauna in the crystal clear water courses was comparatively scarce; although there were some larvae of Odonata and of Coleoptera, only amphipods (Tallitridae) were abundant. In this desert environment, the small streams provided the only habitat where life was found.

DISCUSSION: *Gigantodax eremicus* is closely related to *Gigantodax minor,* described below. The overall structure of the two species is very similar, except for the number of the branches of the respiratory organ of the pupa (13 in *eremicus* and 11 in *minor*) and the somewhat different armature of the hypostomium.

Gigantodax minor, new species
Figures 27A–M, 28A–M, 29A–K, 30A–N, 178B

DIAGNOSIS: *Gigantodax minor* is characterized by the very short second antennal segment in the larva, a strongly sclerotized, pointed, basal appendage of the claw in the female, and a pedunculate pupal gill with 11 branches.

DESCRIPTION: *Female.* Length of wing 2.6–3.4 mm. Head piceous, its pilosity silvery. Antenna and palpus dark brown. Scapus and pedicellus orange. Scutum and scutellum from orange to reddish brown, delicately pruinose. Pleural region from pale yellow to light yellowish brown, faintly pruinose. Thoracic se-

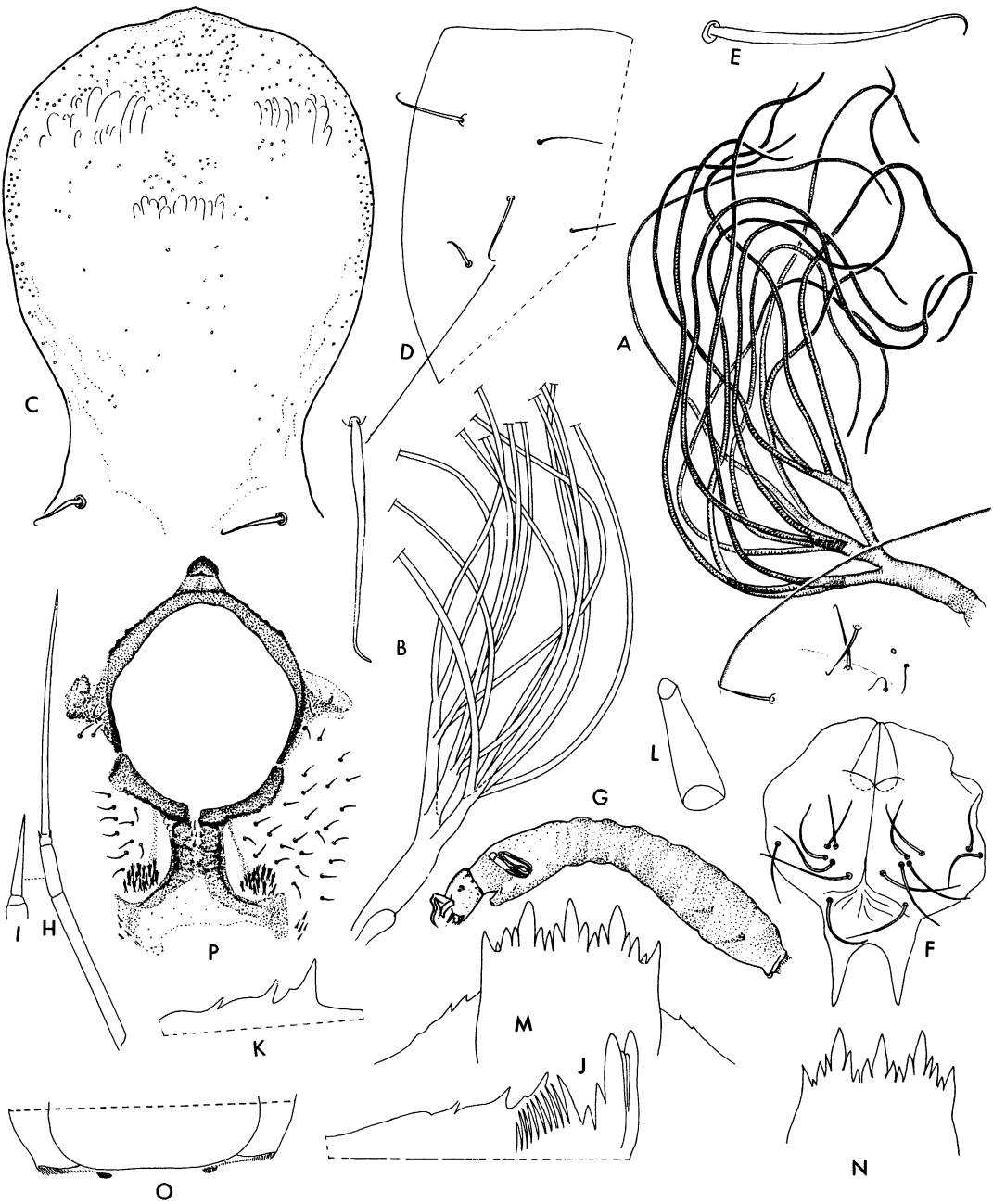

Fig. 26. *Gigantodax eremicus.* A–F. Pupa. **A.** Gill. **B.** Basal portion of different gill. **C.** Frontoclypeus, male. **D.** Portion of thorax, with trichomes. **E.** Anterosublateral trichome. **F.** Distal portion of abdomen. G–O. Larva. **G.** Larva, lateral view. **H.** Antenna, with apical sensillum. **I.** Terminal sensillum of antenna. **J.** Apex of mandible of larva. **K.** Mandibular serrations. **L.** Maxillary palp of larva. **M, N.** Teeth of hypostomium. **O.** Cervical region. **P.** Anal sclerite.

tae golden. Wings translucent, veins light brown. Setae on stem vein golden, with dark tuft at base. Remaining wing setae appearing dark. Legs from entirely pale yellow to light

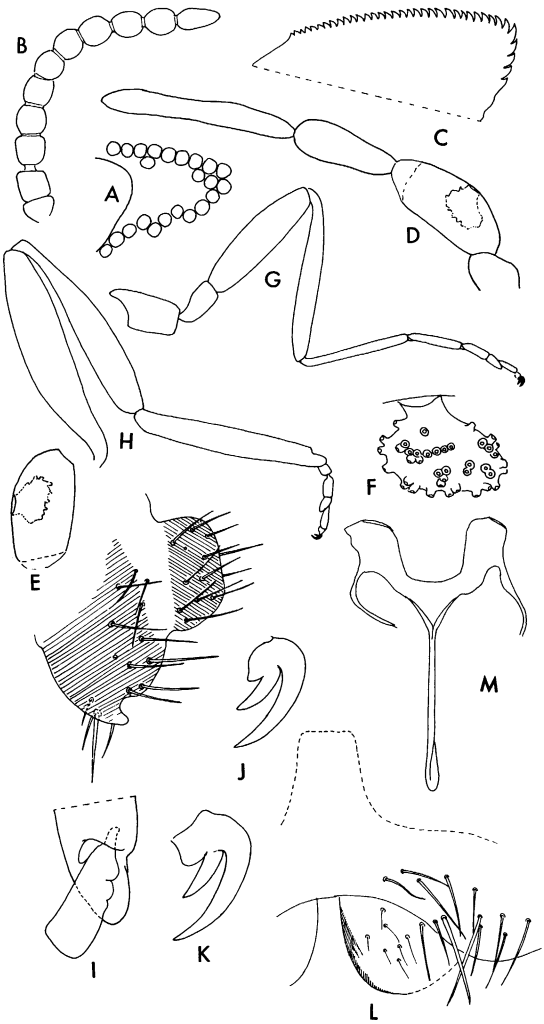

Fig. 27. *Gigantodax minor.* Female. **A.** Fronto-ocular triangle. **B.** Antenna. **C.** Apex of mandible. **D.** Maxillary palp. **E.** Second article of maxillary palp. **F.** Sensorial vesicle. **G.** Foreleg. **H.** Hind leg. **I.** Calcipala with second tarsomere. **J, K.** Claw. **L.** Gonapophyses. **M.** Genital fork.

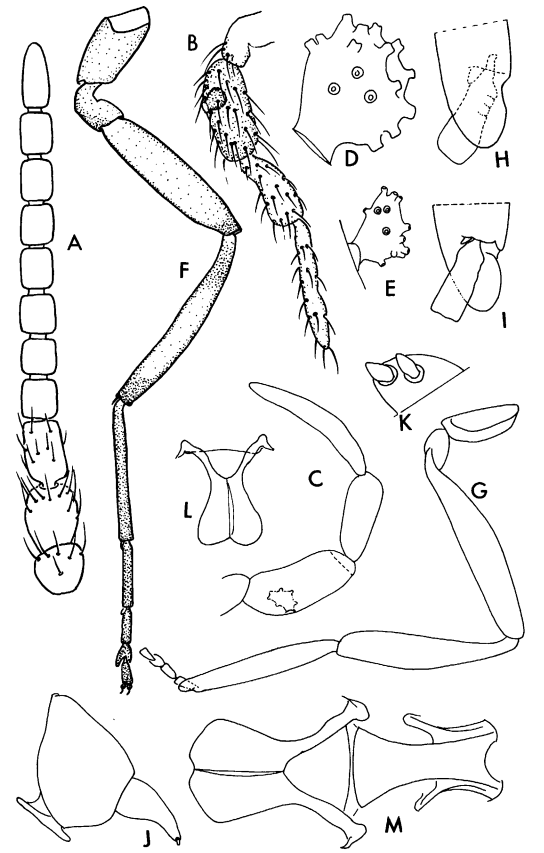

Fig. 28. *G. minor.* Male. **A.** Antenna. **B, C.** Maxillary palp. **D, E.** Sensorial vesicle of maxillary palp (different specimens and magnification). **F.** Foreleg. **G.** Hind leg. **H, I.** Calcipala, with second tarsal article. **J.** Basimere and distimere. **K.** Apex of distimere. **L.** Ventral plate. **M.** Ventral plate and median sclerite.

reddish brown, concolorous or faintly darkened at articulations (best observed in slide mounts). Setae of legs concolorous. Abdominal tergites from dark brown to black, with posterior margin white. Abdominal hairs brass colored.

Frontal angle 40°. Fronto-ocular triangle (fig. 27A) as high as wide. Shape and proportions of antennal segments as shown in figure 27B. Mandible with about 33 teeth on inner and 5 on apical portion of outer border (fig. 27C). Maxilla with approximately 30 teeth. Distal segment of maxillary palp (fig. 27D) twice as long as penultimate. Second segment of maxillary palp suboval (fig. 27E); ratio length to width = 1:0.43–0.56; sensory vesicle of medium size (fig. 27F) with very short neck. Sc with 11–20 hairs, R with setae in two irregular rows; R_1 with setae in one or two rows; spinules absent or at most one or two. R_s almost attaining wing margin. Shape and proportions of fore and hind leg segments as shown in figure 27G, H. Posterior basitarsus 6.9–7.6 times as long as wide. Calcipala as shown in figure 27I. Claws with point-

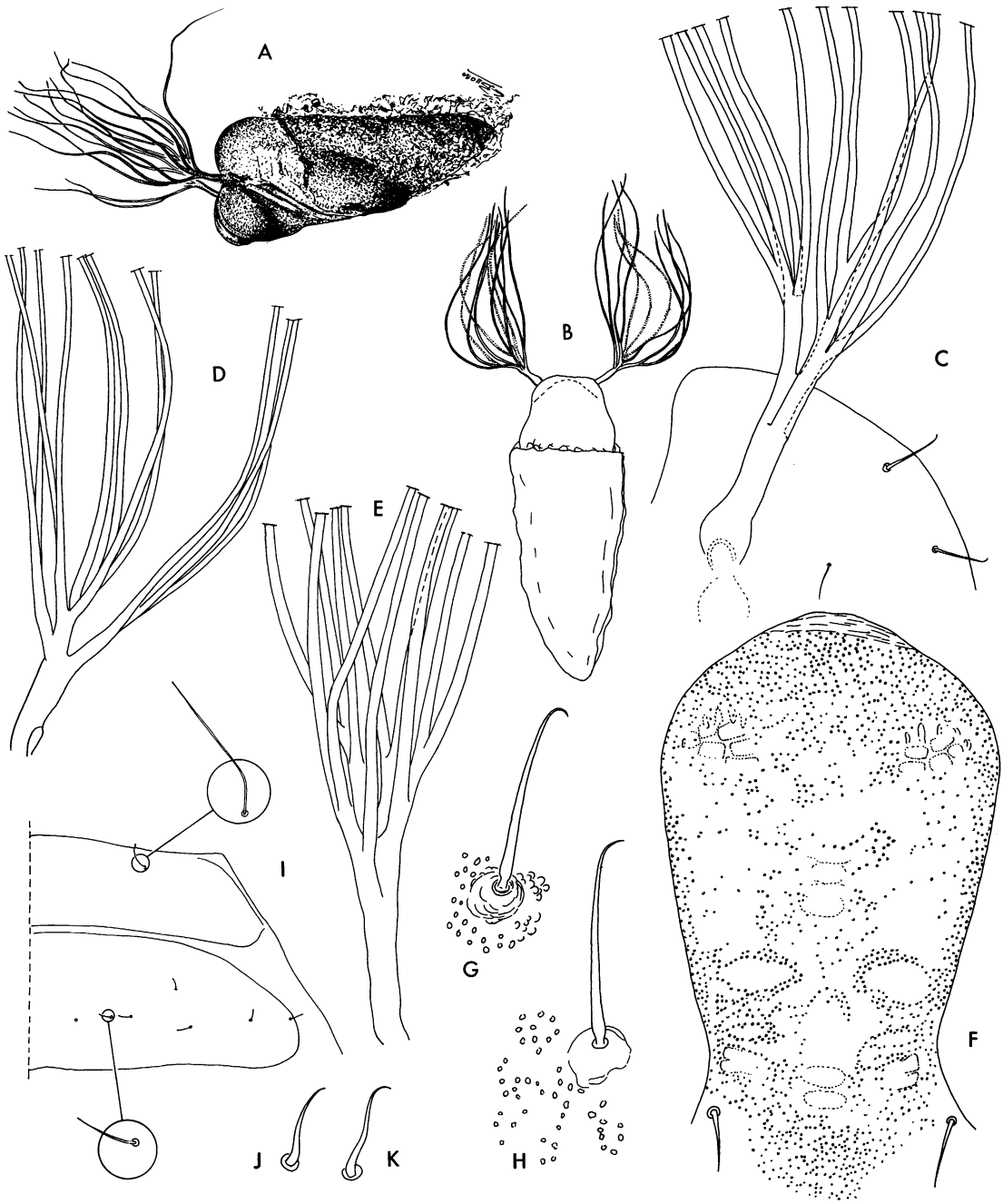

Fig. 29. *G. minor.* Pupa. **A, B.** Pupa in cocoon in lateral and dorsal view. **C.** Portion of thorax, with base of gill. **D, E.** Base of gill. **F.** Frontoclypeus of male. **G, H.** Anterodorsal trichomes of thorax. **I.** Chaetotaxy of abdominal tergites I and II. **J.** Seta of tergite IV. **K.** Seta of tergite VI.

ed projection subbasally (figs. 27J, K, 178B); projection sclerotized as rest of claw. Gonapophyses with short setae (fig. 27L). Genital fork, cercus, and paraproct as illustrated (fig. 27M). Projection of paraproct well developed.

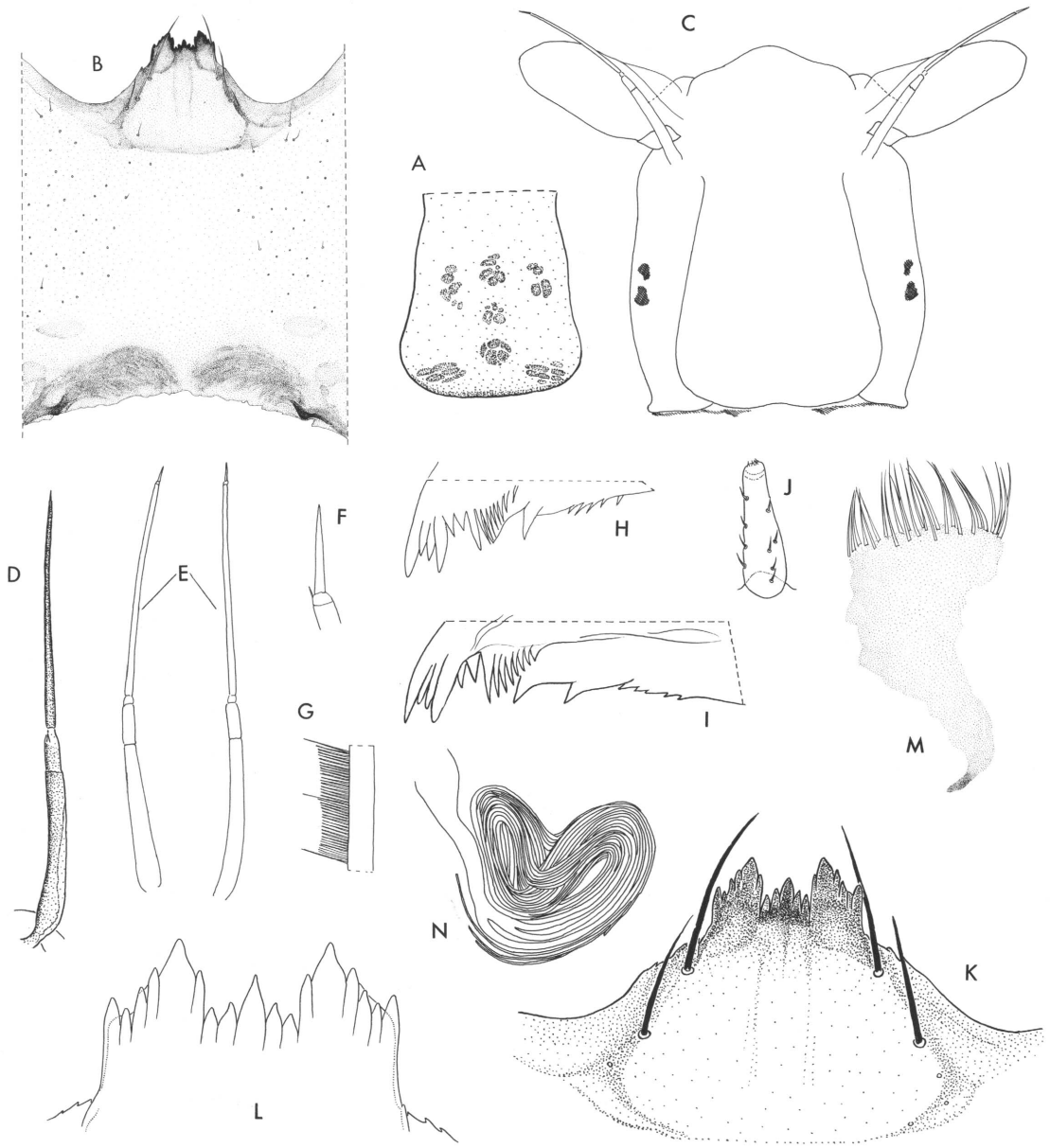

Fig. 30. *G. minor.* Larva. **A.** Cephalic apotome. **B.** Hypostomial bridge. **C.** Head of mature larva, dorsal view. **D, E.** Antennae. **F.** Terminal sensillum of antenna. **G.** Teeth of ray of cephalic fan. **H, I.** Apex of mandible. **J.** Maxillary palp. **K.** Hypostomium. **L.** Toothed portion of hypostomium. **M.** Sclerite of proleg. **N.** Gill histoblast.

Male. Length of wing 3.0–3.5 mm. Color as described for female, but orange color of scutum more intense.

Shape and proportions of antennal segments as shown in figure 28A. Ratio length to width of first flagellomere 1:0.56–0.70. Apical segment of maxillary palp twice as long as subapical (fig. 28B). Sensory vesicle small, from subglobular to ovoid (fig. 28D, E), with short but distinct neck. Chaetotaxy of wing as in female. Fore basitarsus (fig. 28F) 12 times as long as wide, hind basitarsus (fig.

28G) six to seven times as long as wide. Calcipala (fig. 28H, I) covering basal two-thirds of second tarsomere. Distimere about two-thirds the length of basimere, with two apical spines (fig. 28J, K). Main body of basal plate about as long as wide and excavated apically (fig. 28L, M).

Pupa. General aspect as shown in figure 29A, B. Cocoon covering entire abdomen and posterior portion of thorax dorsally, loosely and irregularly woven. Length of body 3.3 mm. Cephalopterothecal length 1.5 mm. Length of respiratory organs approximately 2.5 mm, their general aspect shown in figure 29A–E. Three primary branches inserted close to each other on common elongate stalk, the latter about five times as long as wide. Eleven secondary branches inserted in groups of three or four on very short primary branches. Secondary branches filiform. Frontoclypeus of male with sides almost straight, divergent for most of their length (fig. 29F). Facial trichomes (fig. 29G) slender, in some specimens very small frontal trichome. Thorax with dorsocentral trichomes very slender (fig. 29C); anterodorsal trichomes (fig. 29G–H) stronger, hooked apically. Platelets of thorax minute, more numerous than in female of *eremicus.* Setae of abdominal tergites I and II hairlike, those on tergite II approximately 20 μm long (fig. 29I). Tergites III and IV with 4 + 4 hooks. Setae of tergites IV–VIII hairlike (figs. 29J, K), those of VII 15 μm long. Spinecombs on tergites V–VII, not interrupted, or only once or rarely twice, consisting on tergite VII of 35 spines, their length about 6 μm. Specialized setae of segments VIII and IX simple. Sternites V and VI with 2 + 2 hooks each, VII with 1 + 1 hooks. Hooks of upper and lower surface of abdomen drawn out into a slender filiform point.

Mature larva. Length 5.5 mm. Width of head capsule 0.6 mm, its color whitish. Cephalic apotome with distinct spots (fig. 30A). Hypostomial bridge (fig. 30B) light colored, with pigment along its posterior border and some dark spots on disc. Antenna longer than stem of mouthfan (fig. 30C).

Shape of antenna as shown in figure 30D, E; ratio of length of antennal segments I–III 1:0.20–0.23:1.26–1.38. Terminal sensillum (fig. 30F) 6.5 to 7.0 times as long as wide at base. Cephalic fan with 26–30 large rays, their teeth as shown in figure 30G. Mandible (fig. 30H, I) with seven or eight inner teeth and five or six marginal serrations. Maxillary palp from three to four times as long as wide at base (fig. 30J). Hypostomium as shown in figure 30K, L. Median tooth recessed, not reaching level of apices of corner teeth; line connecting apex of fourth lateral to apices of corner teeth meeting at right angle. Hypostomium with two or three minute serrations, and with two hypostomial setae in each row. Cervical sclerites in shape of very narrow transversal bands, not fused at middle (fig. 30C). Proleg sclerite with about 26 teeth (fig. 30M). Histoblast dark, its structure shown in figure 30N. Perianal scales conspicuous, arranged in one tuftlike group on each side of base of anal sclerite, not forming circumanal ring. Recurrent struts not perceptible. Crochet ring with 77–86 rows composed of 18–20 teeth each.

HOLOTYPE: CHILE: *Talca:* Alto de Vilches, 1200 m, Oct. 30, 1966 (J. Rozen and L. Pena; AMNH), female.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 male allotype, 52 females, and 21 male paratypes; AMNH. *Aysen:* Lago Frio, Coihaique, Valley of Rio Simpson, Jan. 20–23, 1961 (L. Pena; CNC), 1 female; Rio Maniguales, Jan. 26–28 (L. Pena; CNC), 1 female. *Chiloe:* Dalcahue, Feb. 1–8, 1962 (L. Pena; CNC), 1 female. *Valdivia:* Pucon, Feb. 1967 (S. Coscarón; AMNH), 4 larvae. *Malleco:* Curacautin, Dec. 17, 1959 (L. Pena; CNC), 2 females. Rio Blanco, 1100–2000 m, Feb. 1964 (L. Pena; CNC), 1 female. *Bio-Bio:* El Abanico, Dec. 31, 1950 (E. Ross and A. E. Michelbacher; CAS), 1 female. *Nuble:* 40 km E of San Carlos, Dec. 23–24, 1950 (E. Ross and A. E. Michelbacher; CAS), 17 males, 39 females. *Linares:* Las Cruces, Oct. 1958 (L. Pena; CNC), 2 females; Fundo Malcho, Dec. 1957 (L. Pena): 1 male. *Talca:* Oct. 5, 1972 (P. Wygodzinsky, S. Coscarón, and L. Pena), 3 males, 5 females; 5 km W of Vilches, 615 m, Jan. 13, 1967 (M. E. Irwin, L. A. Stange; CIS), 15 males, 6 females; ibid., Jan. 26–28, 1964 (L. Pena; CNC), 4 females. *Curico:* Estero la Jaula, Jan. 1964 (L. Pena; CNC), 2 females. El Coigual, Jan. 20–26, 1964 (L. Pena; CNC), 3 females, 1 male. Rio Claro, Oct. 9, 1966 (E. Schlinger; CIS), 1 male, 1 female. *O'Higgins:* Bosque de los Conser-

vadore, Graneros, 1100 m, March 1–4, 1962 (L. Pena; CNC), 9 males, 6 females. *Santiago:* Cuesta La Dormida, Nov. 1, 1966 (E. Schlinger; CIS), 2 females; El Canelo, Jan. 10, 1967 (E. Schlinger; CIS), 1 male, 4 females; Quebrada de la Plata, Rinconada, Maipu, April 26, 1966, April 27, 1966, June 2, 1966, August 15, 1966, August 22, 1966, Sept. 10, 1966, Sept. 10, 1966, Oct. 8, 1966, Oct. 26, 1966 (Irwin; CIS), 4 males, 8 females; Cerro El Roble, Dec. 28–31, 1943 (L. Pena; CNC), 2 females; road from Runge to Cerro El Roble, Oct. 11, 1972 (L. Pena, P. Wygodzinsky), 1 pharate female, 2 pupae, 3 larvae; Cerro El Roble, Dec. 29–31, 1963 (L. Pena; CNC), 1 female. *Aconcagua:* Cuesta Alicauhe, Ovalle, 1300 m, Nov. 15–16, 1959 (L. Pena; CNC), 1 female. *Coquimbo:* Majada Blanca, Manquehua, Combarbala, Aug. 2–8, 1960 (L. Pena; CNC), 1 female, 1 male mounted on slide. Hacienda Illapel, Nov. 1–6, 1954 (L. Pena; CNC), 6 males. ARGENTINA: *Rio Negro:* Bariloche, Playa Linda, June 26, 1983 (S. Coscarón; MLP), 1 male, pupae and larvae. *Neuquen:* Pucara, Lanin National Park, Feb. 20, 1967 (S. Coscarón; MLP), 1 male, 5 larvae.

ETYMOLOGY: In reference to the small body size.

DISCUSSION: The color of the adult specimens of *G. minor* which we have examined is far from uniform, especially as to the intensity of the orange portions of the thorax and the legs. However, examining relatively large numbers of specimens collected at the same time and in the same place showed us that the variation in color intensity is entirely due to preservation.

Gigantodax minor occupies a large area, and it is surprising that the species was apparently not found among the Chilean and Patagonian *Gigantodax* species studied by Edwards (1931).

Gigantodax bolivianus Enderlein
Figure 31A–N

Gigantodax bolivianus Enderlein, 1925: 205; 1928: 10; 1930: 84.
Gigantodax boliviensis: Enderlein, 1930: 91.
Simulium (Gigantodax) bolivianum: Edwards, 1931: 131. Pinto, 1931: 680.
Simulium bolivianum: Vargas, 1945: 120.
Gigantodax bolivianum: Smart, 1945: 499. Vulcano, 1967: 3; 1981: 276. [Incorrect gender.]

DIAGNOSIS: Reddish brown species, with basal claw tooth hook-shaped; largest of known *Gigantodax* species.

REDESCRIPTION: *Female.* Length of wing 7.0–7.4 mm. Head including clypeus dark gray; pilosity brass colored. Antenna and palp dark gray; scapus, pedicellus, and extreme base of first flagellomere orange. Scutum, scutellum, metanotum, and pleuron reddish brown. Thoracic setae brass colored. Wing translucent except distinctly yellowed area between Sc and R; veins light brown. Hairs on stem vein and on rest of veins dark. Halter light brown. Legs very light yellowish brown. Abdominal terga piceous, with hind margin whitish, narrow on anterior, somewhat wider on posterior segments. Abdominal hairs brass colored.

Frontal angle very narrow, estimated at 50° or less. Fronto-ocular triangle slightly higher than wide. Antenna not examined in detail, similar to those of females of other species of genus. Mouthparts not examined in detail, but mandible with well-developed teeth on inner margin; high degree of sclerotization of mouthparts indicative of normal function. Sc with approximately 40 setae. R with setae in one or two close rows along hind border of vein. R_1 with two irregular rows of setae; spinules present, much less numerous than setae, beginning at level of insertion of Sc on C. R_s with setae on dorsal surface on apical portion only, arranged in one row; undersurface with setae arranged in three rows. A_1 falling short of wing margin, almost straight apically (fig. 31A). Shape and proportions of some segments of legs as shown in figures 31B–E. Hind basitarsus 12 times as long as wide. Calcipala rounded, notched at base, extending very slightly beyond middle of second tarsomere (fig. 31E, F). Basal tooth of claws hook-shaped, rather wide at base, its distance to apex of claw equal to its length (fig. 31G–I). Abdominal tergal plates as shown in figure 31J, sterna with delicate setae only. Eighth sternite with 1 + 1 elongate groups of approximately 50 setae, four or five of these distinctly longer and stouter than the remaining (fig. 31K); gonapophyses separated from each other only by short distance, membranous, with very numerous microtrichia and a few short setae; inner margins of gonapophyses more strongly sclerotized. Genital fork as shown in figure 31M, without special

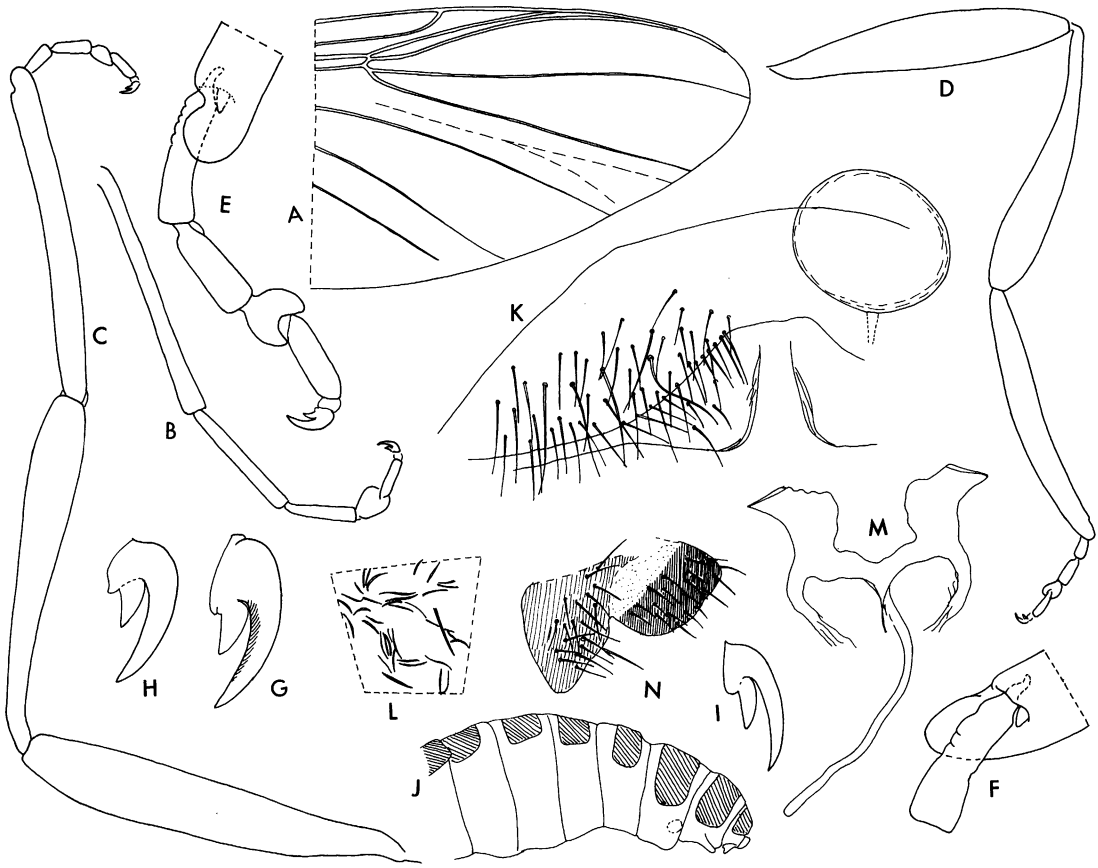

Fig. 31. *Gigantodax bolivianus.* Female. **A.** Portion of wing. **B.** Tarsites of forelegs. **C, D.** Hind legs. **E.** Calcipala, with remaining tarsal segments. **F.** Calcipala, with second tarsal segment. **G–I.** Claws. **J.** Abdomen, lateral view. **K.** Portion of eighth sternite, with spermatheca and gonapophyses. **L.** Microstructure of spermatheca wall. **M.** Genital fork. **N.** Cercus and paraproct. (Lectotype: B, C, E, G, H, L; paralectotype: A, M, N; not a type: D, I, J, K).

characters. Spermatheca subglobular (fig. 31K), strongly sclerotized throughout, area of insertion of sperm duct wrinkled. Interior surface of spermatheca delicately rugose, with a few scattered elongate spicules (fig. 31L). Paraproct and cercus as shown in figure 31N.

Male, pupa, and larva. Unknown.

MATERIAL EXAMINED: Two females from type series, labeled: Cuesta von Cillunticara, Bolivia, 3500 m. Coll. Fassl/Type *Gigantodax bolivianus* Type Enderlein Female / Dr. Enderlein det. 1925. One female is here designated lectotype, the other one paralectotype (Naturhistorisches Museum, Vienna).

DISCUSSION: According to Enderlein's description, the original material of this species was deposited in the Berlin and Vienna museums. The species cannot be found in the Berlin Museum, but three females kept at the Naturhistorisches Museum of Vienna were examined. All three specimens are labeled as indicated in the preceding paragraph, but they belong to more than one species. Two females—those described above in detail—are characterized by their extraordinarily large size (wing length 7.0 mm or more), their very long hind basitarsus, which is 12 times as long as wide, and the rounded, basally notched calcipala, which extends only slightly beyond the middle of the second tarsomere. The remaining female is much smaller (wing length 5.8 mm), its hind basitarsus is comparatively shorter, being only nine times as long as wide, and the calcipala is subelliptical in shape, extending conspicuously beyond the middle of the second tarsomere. These differences as

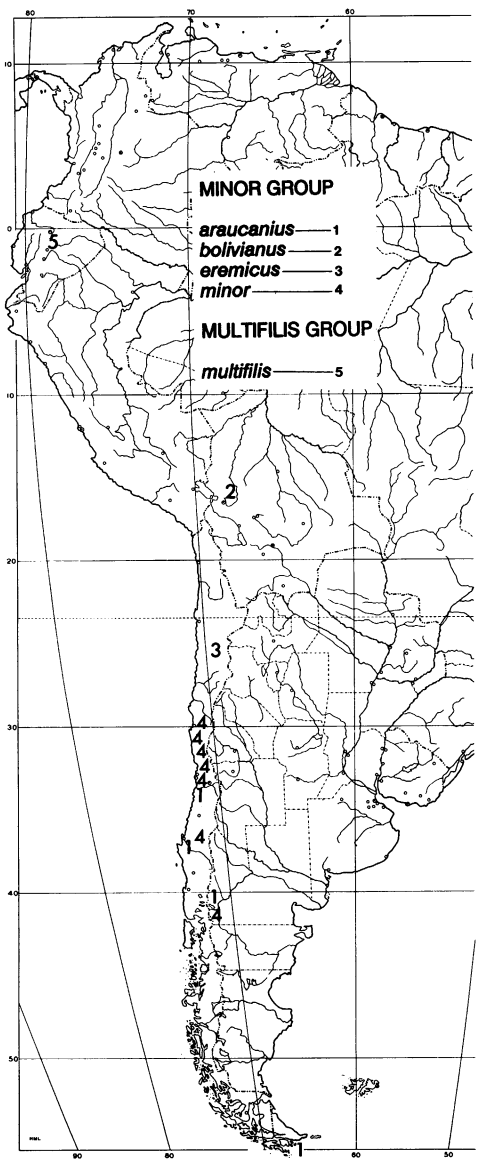

Fig. 32. Map with the distribution of species of the *minor* and *multifilis* groups.

observed in specimens of the same sex, collected presumably at the same time and the same location, indicate specific differences. In order to fix the concept of *G. bolivianus,* we are designating and thus labeling the better preserved of the two large specimens as lectotype, and the second as paralectotype. The smaller specimen probably belongs to a yet unnamed species.

One important character shared by all three specimens is the hooklike tooth of the claw, found in approximately similar form only in some austral species of the genus: *ignigulus, araucanius,* and *minor.* Because of the structure of the gonapophyses, spermatheca, and genital fork, we consider *bolivianus* to be close to the *minor* species group, where we have tentatively placed it.

Wygodzinsky (1958) erroneously identified a Peruvian species of *Gigantodax* as *bolivianus*; it is redescribed here as *Gigantodax herreri,* new species.

multifilis group

DIAGNOSIS: The *multifilis* group is recognized by the peculiar multiple lobules of the larval anal gills, the multiple terminal filamentous branches in the pupal gills, the reduced sensory organ of the maxillary palp, and the subtriangular subbasal tooth in the female claw.

FEMALE: Dark brown coloration; frons, eye, antenna, and maxillary palp normal. Sensory organ of maxillary palp poorly developed (fig. 33C). Mandible with teeth on only one side. Scutum with only recumbent hairs; R_1 with spinules. Calcipala well developed, longer than half of the length of second tarsomere. Subbasal tooth of claw subtriangular (fig. 33I). Genital fork and cercus elongated, paraproct normal; subcircular in shape (fig. 33J).

MALE: Color as in female. Ventral plate without apical excavation; aedeagal membrane without spinules.

PUPA: Cocoon well developed. Gill branches aborescent, with over 100 terminal filaments (figs. 34, 35A–C). Frontoclypeus with only facial trichomes, and trichomes on the frontoclypeus and thorax not hooked distally. Abdominal tergite I with 3–5 hairy trichomes on each side (fig. 35H). Terminal hooks thin and elongated (fig. 35K).

LARVA: Body cuticle without hairs, overall color dark. Cephalic apotome widest near base (fig. 36A). Antenna longer than stem of cephalic fan. Terminal sensillum elongated (ratio length/width over 6) (fig. 36D); marginal serrations of mandible reduced (3–6) (fig. 36F–I). Hypostomium with median tooth below level of corner teeth (fig. 36K). Ventral pa-

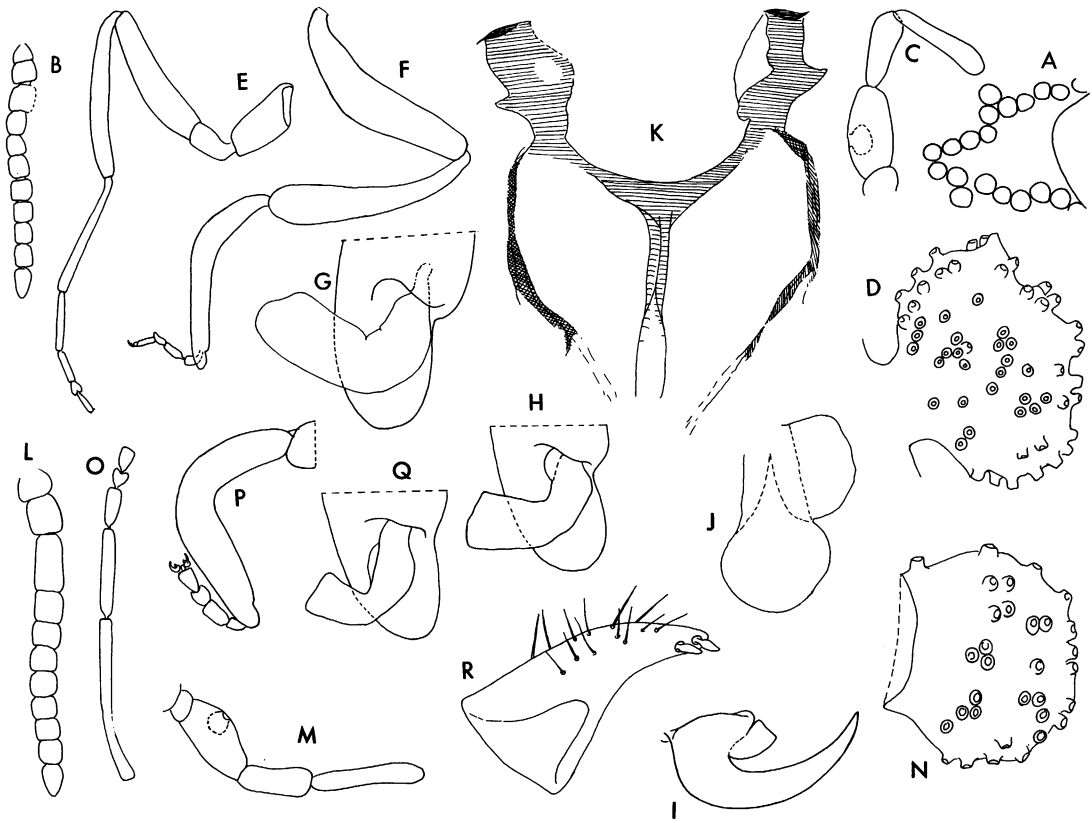

Fig. 33. *Gigantodax multifilis.* A–K. Female. **A.** Fronto-ocular triangle. **B.** Antenna. **C.** Maxillary palp. **D.** Sensory vesicle. **E.** Foreleg. **F.** Hind leg. **G, H.** Calcipala, with second tarsal segment. **I.** Claw. **J.** Cercus and paraproct. **K.** Genital fork. L–R. Male. **L.** Antenna. **M.** Maxillary palp. **N.** Sensory vesicle; same scale as D. **O.** Tibia and tarsi of foreleg. **P.** Tarsus of hind leg. **Q.** Calcipala, with second tarsal segment. **R.** Distimere.

pilla of body prominent. Anal scales not forming a complete circumanal ring.

DISTRIBUTION: Known by only one species from one locality in Ecuador (fig. 32).

DISCUSSION: This group is recognized by a peculiar character that is present only in Simuliini larvae: the presence of more than 20 elongated lobules in the anal gill. This group also possesses several features in common with other groups. For example, the pupal gill is aborescent with numerous filamentous branches as in the *cortesi* and *igniculus* groups, but *multifilis* group species have filament apices widened and rounded. Also there is a reduced number of setae on abdominal tergite I, elongated terminal spines in the pupa, elongated terminal sensillum on the antenna, and reduced marginal serrations on the mandible in the larva (these characters are in common with the *minor* group). The *multifilis* group has in common with some recently derived *Gigantodax* a reduced, subtriangular shape of the basal tooth claw (also seen in *Araucnephia,* which we attribute to parallel evolution).

Gigantodax multifilis, new species
Figures 33A–R, 34, 35A–K, 36A–O

DIAGNOSIS: Differs from all known species with triangular process of the claw of the female by the very large number of respiratory filament branches of the gill of the pupa and the anal gill of larvae with multiple lobules.

DESCRIPTION: *Female (not well preserved).* Wing length about 3.8 mm. Head dark; clyp-

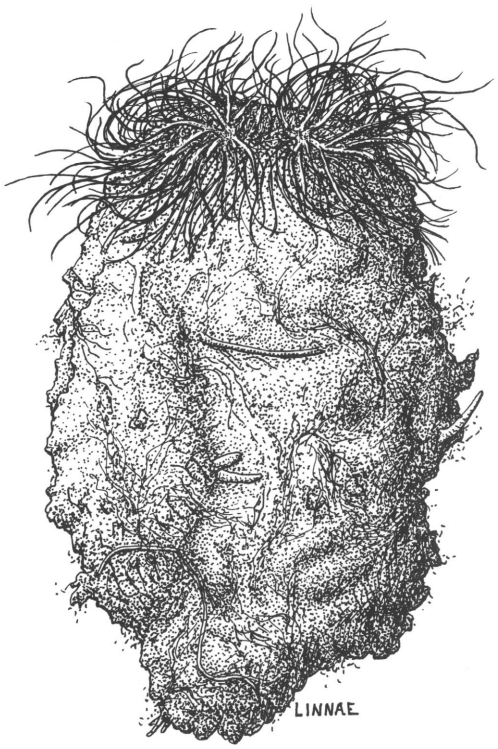

Fig. 34. *G. multifilis.* Pupa in cocoon.

eus and mouthparts brownish. Antenna reddish brown, scapus and pedicellus faintly lighter. Setae of postocciput brass colored. Scutum and scutellum dark reddish brown; metanotum piceous. Pleura and sterna pale brown. Legs light reddish brown. Halter orange yellow at base, pale yellowish white on stem and capitulum. Wing with veins light brown, hairs on stem vein and other veins piceous.

Frontal angle 40°. Fronto-ocular triangle about as high as wide (fig. 33A). Shape and proportions of antennal segments as shown in figure 33B. Mandible with teeth only on inner margin, their number 26–28. Maxilla with 26–27 teeth. Last segment of maxillary palp only slightly longer than penultimate (fig. 33C). Second segment shortly suboval, ratio length/width = 1:0.54–0.57. Sensory vesicle shortly oval, not significantly larger than that of male, with distinct short neck (fig. 33D); Sc with hairs in one row. R with setae basally in one, apically in several rows. R_1 with setae in one row, intermixed with spinules arranged in one or two rows, apparently beginning apicad of level of insertion of Sc on C; where present, spinules more numerous than setae. R_s with setae on upper surface in one, on undersurface in several series. Approximate shape and proportion of leg segments as shown in figure 33E, F. Hind basitarsus about 7.4 times as long as wide. Calcipala more than half the length of second tarsomere (fig. 33G, H). Basal tooth of claw comparatively small (fig. 33I). Eight abdominal sternite with delicate hairs only. Genital fork as shown in figure 33K, cercus and paraproct as in figure 33J. Gonapophyses similar to that of *araucanius,* lobulate with about 12 chaetae. Spermatheca well sclerotized.

Pharate male. Length of wing and color unknown. Holoptic. Shape and proportions of antennal segments as shown in figure 33L; ratio length/width of first flagellomere 1:0.5. Distal segment of maxillary palp (fig. 33M) somewhat longer than penultimate. Sensory vesicle subglobular, about as large as that of female, with large opening but without distinct neck (fig. 33N). Wing similar to those of female. Approximate shape and proportions of leg segments as shown in figure 33O, P. Fore basitarsus 12.8 times, hind basitarsus about 16.0 times as long as wide. Calcipala extending beyond center of second tarsomere (fig. 33Q). Genitalia without special characters; distimere (fig. 33R) over two-thirds as long as basimere. Main body of ventral plate as long as wide.

Pupa. Cocoon baglike, completely covering body of pupa except gills (fig. 34). Weave of cocoon very loose, cocoon completely covered by layer of minute, mostly organic particles. Length of cocoon 5.5 mm. Length of body of pupa 5 mm; cephalopterothecal length 3.2 mm.

Gills as shown in figure 35A–C, consisting of four basal trunks, divided at and near their bases into secondary branches, the latter subdivided again progressively, terminating in more than 100 slender respiratory filaments. Basal portion of gill perpendicular to longitudinal axis of body of pupa, basal trunks diverging, forming a forwardly facing structure, apical branches and respiratory filaments directed forward. Surface of branches and respiratory filaments minutely pitted; apex of filaments slightly widened, rounded

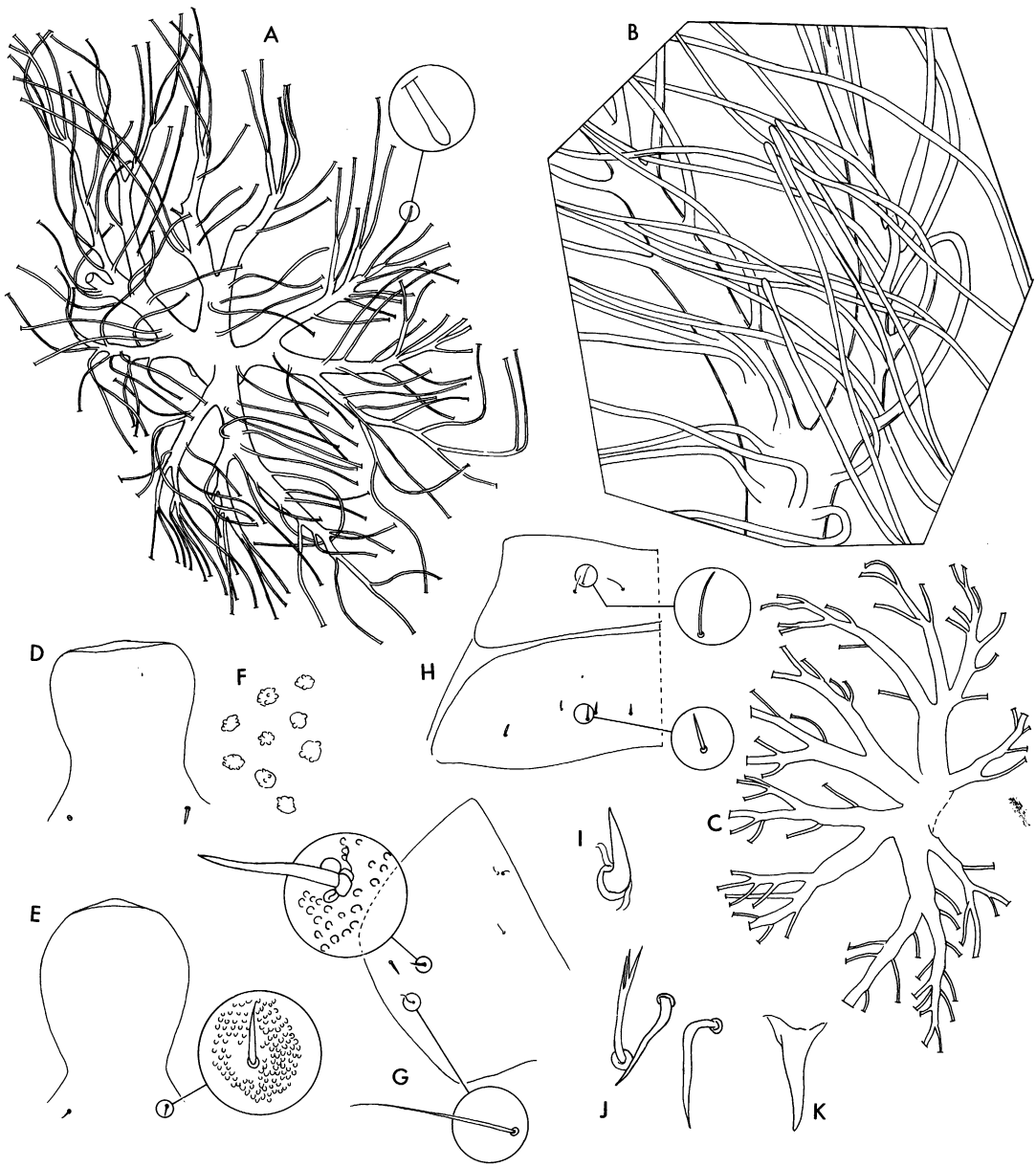

Fig. 35. *G. multifilis*. Pupa. **A.** Gill, not all filaments shown. **B.** Detail of gill. **C.** Portion of basal gill. **D.** Outline of frontoclypeus, female. **E.** Same, male. **F.** Platelets of frontoclypeus. **G.** Portion of thorax, with trichomes. **H.** Chaetotaxy of abdominal tergites I and II. **I.** Hook of tergite IV. **J.** Specialized setae of distal portion of abdomen. **K.** Terminal spine of abdomen.

distally. Shape and proportions of frontoclypeus of female and male pupae as shown in figure 35D, E, with numerous very regularly distributed verrucose platelets (fig. 35F). Facial trichomes short, spinelike. Thorax with platelets on dorsum similar in structure and arrangement to those of frontoclypeus. Dorsocentral trichomes consisting of two strong spinelike and one hairlike seta (fig. 35G); dorsolateral trichomes obsolescent, in shape of fine hairs difficult to perceive. Setae of abdominal tergite I hairlike, their length 70–90

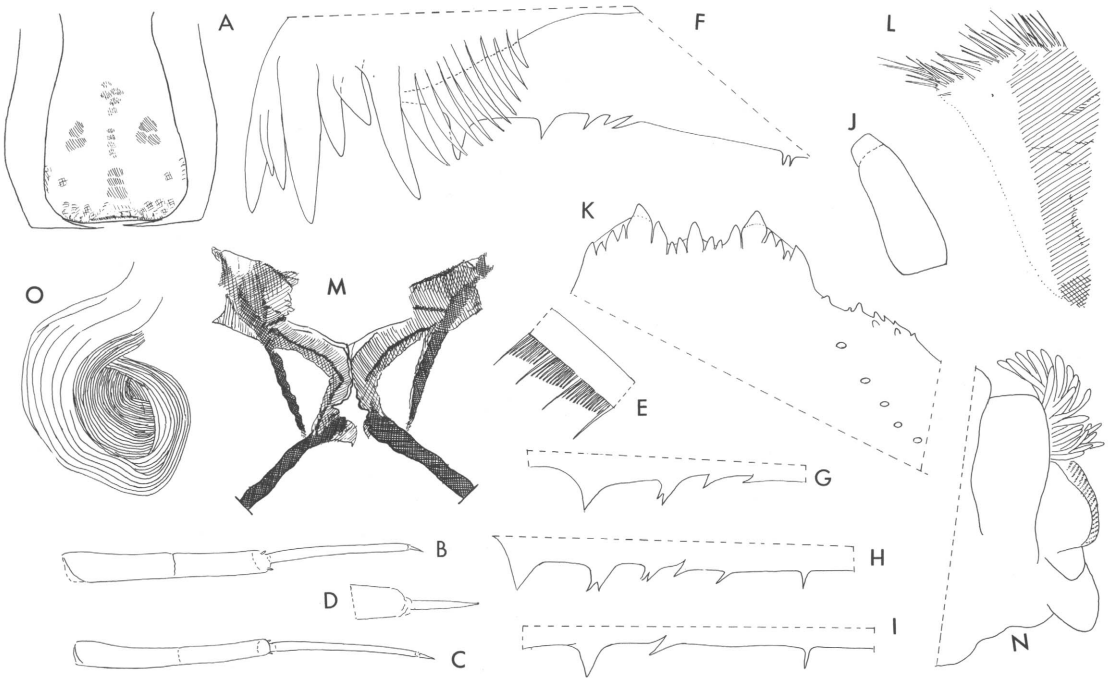

Fig. 36. *G. multifilis.* Larva. **A.** Head, dorsal view. **B, C.** Antenna. **D.** Terminal sensillum of antenna. **E.** Teeth of ray of cephalic fan. **F.** Apical portion of mandible. **G–I.** Mandibular serrations. **J.** Maxillary palp. **K.** Part of hypostomium. **L.** Sclerite of proleg. **M.** Anal sclerite, most of ring-shaped portion removed. **N.** Posterior portion of abdomen of larva, side view. **O.** Gill histoblast.

μm; setae of tergite II spinelike and much shorter, 20–30 μm (fig. 35H). Tergites III and IV with 4 + 4 short hooks (fig. 35I). Anterodorsal setae short, spiniform. Setae of tergites V–VIII inconspicuous and very short, not more than 30 μm long. Spine-combs on tergites VI–VIII continuous, on tergite VII consisting of 40–48 spines, their length 15–20 μm, viz., over one-half to two-thirds as long as setae of this segment. Specialized setae of segments VIII and IX simple, from straight to variously curved, some apically bifurcate or trifurcate (fig. 35J). Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks, one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous. Terminal hooks thin and elongated (fig. 35K).

Mature larva. Length 7.0–8.0 mm; width of head capsule 0.75 mm. Body shape as usual for genus; ventral papillae very prominent. Overall color of larva dark, pigment most intense on lower surface of anterior portion of body; dark color due to hypodermal pigment. Head light brown; spots of cephalic apotome distinct (fig. 36A). Hypostomial bridge slightly darker than surrounding areas, with medial longitudinal stripe lighter colored. Antenna faintly pigmented, third segment not darker than remaining. Shape of antenna as shown in figure 36B, C; ratio of segments I–III = 1:0.68–0.74:1.24–1.30. Terminal sensillum 6.5–7.0 times as long as wide at base (fig. 36D). Cephalic fan with 29–37 large rays, their teeth normal (fig. 36E). Mandible (fig. 36F–I) with 10–11 inner teeth and three to six marginal serrations; in many cases, these serrations very remote from remaining ones. Maxillary palp stout, from 2.5–2.9 times as long as wide at base (fig. 36J). Hypostomium as shown in figure 36K; median tooth not reaching level of apices of corner teeth, but slightly surpassing level of apices of third intermediate teeth (fig. 36K). Line connecting apices of fourth lateral teeth and corner teeth intersecting at angle of about 100°. Hypostomium with 9–11 lateral serrations, some of

which form double rows, and five to six hypostomial setae in each row. Sclerite of proleg about 37 hooks (fig. 36L). Gill histoblast approximately as shown in figure 36O, characterized by very large number of respiratory filaments. Perianal scales obsolescent, except a few weakly pigmented small scales near upper arms of anal sclerite; no others perceptible. Recurrent struts well developed, strongly pigmented (fig. 36M). Crochet ring with 105–110 rows of 21–22 hooks each. Rectal gills subdivided into numerous secondary lobules (fig. 36N).

HOLOTYPE: ECUADOR: *Pichincha:* highway from Aloag to Santo Domingo de los Colorados, W slope of mountain range, 2650 m, Aug. 9 and 19, 1969 (P. and B. Wygodzinsky; AMNH), female (reared, with associated pupal exuviae).

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, one male and one female (pharate, with associated pupal exuvia), paratypes, pupae, and larvae.

ETYMOLOGY: The specific name is taken from the Latin *multus,* much, and *filum,* thread, an allusion to the very numerous branches and slender respiratory filaments of the gills of the pupa.

BIOLOGY: The aquatic instars were found in an area of montane cloud forest in a very small roadside stream (less than 1 ft wide) originating from water dripping over a cliff; the location was partly shaded by forest. Pupae were located on the undersides of stones in the stream, and were very difficult to recognize because of the mud.

DISCUSSION: The outstanding characters of this species are the large number of branches and respiratory filaments of the pupal gills, the almost complete lack of sexual dimorphism in the size of the sensory organ of the maxillary palp of the adults, and the numerous secondary lobules of the rectal gill of the larvae. The last character is unique in the genus; all other species of *Gigantodax,* and, in fact, all known Prosimuliini, have simple trilobed rectal gills. The pupal gill is quite similar in general structure to that of *G. igniculus.*

brophyi group

DIAGNOSIS: Recognized by the presence in the pupa of 18 filamentous gill branches not flexible basally and tapering gradually, without cuticular processes; subbasal tooth of claw subtrapezoidal in shape in the female, and the median hypostomial tooth is below the level of the corner teeth in larvae.

FEMALE: Brownish to yellow medium-size species. Frons, eye, antenna, and maxillary palp normal. Sensory organ of basal article of maxillary palp well developed. Mandible with teeth only on internal border. R_1 with spinules or only spiniform setae. Calcipala well developed, length variable, from less than half to more frequently distinctly surpassing half the length of second tarsomere. Subbasal tooth of claw subrhomboidal (fig. 178C). Gonapophyses generally with only a few setae, distal border straight, at same level as posterior border of eighth sternite. Genital fork with posterior arms wide and parallel. Spermatheca subspherical, of normal size.

MALE: Color as in female or slightly darker. Holoptic (except *femineus*), without frontoocular triangle. Ventral plate without distal concavity and aedeagal membrane without spinules.

PUPA: Cocoon well developed. Gill branches of variable orientation but of about same length, slender basally. Frontoclypeal trichomes not hooked distally. Abdominal tergite I with about 5 + 5 trichomes of similar size. Setae of segments VIII–IX generally simple. Terminal hooks stout.

LARVA: Cuticle without setae. Cephalic apotome widest near base. Antenna shorter than or as long as the stem of cephalic fan, with terminal sensillum not distinctly elongated (ratio length/width = 1:4.0–5.5). Ratio of segments normal (second segment a little shorter than first, third shorter than first and second combined). Mandible with numerous marginal serrations (6–14). Hypostomium with median tooth below level of corner teeth. Recurrent struts well developed. Anal scales forming a complete circumanal ring. Anal gill with three lobes.

DISTRIBUTION: From Venezuela to Tierra del Fuego (fig. 80).

DISCUSSION: Peculiar to this group are a pupal gill with 18 filamentous branches of approximately equal length, that are smooth and not flexible basally, and the subtrapezoidal shape of the subbasal claw tooth in females. The number of branches is here very

fixed except in the hard, modified gills of the most recently derived species of *wrighti* group. The subbasal tooth shape is similar to *Cnesia,* and it could be derived from the subtriangular or subrhomboidal tooth shape present in the most plesiomorphic Neotropical Prosimuliini.

Gigantodax brophyi (Edwards)

Figures 37A–S, 38A–P, 39A–I, 40A–K

Simulium (Gigantodax) brophyi Edwards, 1931: 133. Orfila, 1935: 1528. Vargas and Diaz Najera, 1951a: 156.

Gigantodax brophyi: Wygodzinsky, 1961a: 460; 1961b: 564. Vulcano, 1967: 16; 1977: 290.

Gigantodax bonorinorum Coscarón and Wygodzinsky, 1962: 284. NEW SYNONYMY.

DIAGNOSIS: This species can be recognized by the combination of the calcipala which is shorter than half the length of the second metatarsal segment, the absence of spinules on R_1, the patches of black setae on the stem vein and base of the costa, and the pupal gill with arborescent blackish branches.

DESCRIPTION: *Female.* Length of wing 4.8–5.0 mm. Frons and clypeus light brown, maxillary palp black. Frons and clypeus with silvery pilosity. Vertex and posterior margin of head with silvery setae. Scapus and pedicellus light brown, flagellum dark brown. Scutum and scutellum from orange to reddish brown with brass-colored hairs. Scutum in some cases with percurrent, dark, parallel-sided band. Shoulders yellowish. Posterior border of scutum and scutellum with numerous large light brown semierect setae. Metanotum yellowish brown, with silvery pruinosity. Pleura brownish violaceous, pruinose. Halter pale grayish brown, with dark capitulum. Wing uniformly pale gray, veins light brown, their setae black. Legs light brown, faintly darkened on apical third, their setae concolorous. Abdomen light brown; hind border of tergites whitish. Abdominal fringe silvery.

Frontal angle 65°. Frons as in figure 37A–C. Fronto-ocular triangle about as high as wide (fig. 37G). Shape and proportions of antennal segments as illustrated (fig. 37E, F). Mandible with 20–23 teeth. Maxilla with 29–35 teeth. Terminal segment of maxillary palp twice as long as penultimate. Second segment of maxillary palp (fig. 37H) swollen, ratio length/width = 1:0.61–0.68, slightly less than twice as long as terminal segment. Sensory vesicle (fig. 37I) spherical, with distinct neck, occupying one-third total length of article. Base of hypopharinge as shown in figure 37J. Sc with 32–38 setae, not extending beyond level of distinct curvature of Sc. R with setae in two or three rows, the distal ones heavily sclerotized in some specimens, but not considered as spinules. Shape and proportions of fore and hind legs as shown in figure 37K, L. Hind tarsal segments as shown in figure 37M, N; hind basitarsus seven times as long as wide. Calcipala not attaining level of middle of second tarsomere (fig. 37O). Basal tooth of claw not heavily sclerotized (fig. 37P, Q). Eighth sternite with gonapophyses, cercus, paraproct, genital fork (fig. 37S) and spermatheca (fig. 37R) as illustrated. Sclerotization of spermatheca terminating abruptly at insertion of spermathecal duct.

Male. Holoptic. Length of wings 4.2–4.5 mm. Color as in female, but orange or reddish areas more intensely colored in many cases. Shape and proportions of antennal segments as shown in figure 38D. First flagellomere cylindrical, as long as wide. Terminal segment of maxillary palp twice as long as penultimate (fig. 38E). Sensory vesicle (fig. 38F) smaller than in female, occupying about one-fifth of total length of penultimate segment of palp. Katepisternum as shown in figure 38G, H. Chaetotaxy of wing as in female. Shape and proportions of tarsomeres of hind legs as shown in figure 38I, J. Hind basitarsus about six times as long as wide. Calcipala not attaining level of middle of second tarsomere (fig. 38K). Genitalia as illustrated (fig. 38L–P). Membrane of aedeagus with numerous spicules. Median sclerite well developed, proximal portion widened posteriorly with transverse branch. Distimere twice as long as basimere, with two apical spines. Main body of basal plate slightly wider than long.

Pupa. Cocoon small, covering pupa from base of abdomen to head, leaving only respiratory organ free (fig. 39A, B). Cocoon very light brown, loosely woven, translucent. Length of cocoon along dorsum up to 4.1 mm. Cephalopterothecal length 3.2–3.6 mm. Respiratory organs dark brown, consisting of slender filamentous branches originating from four very short stalks, the latter inserted on

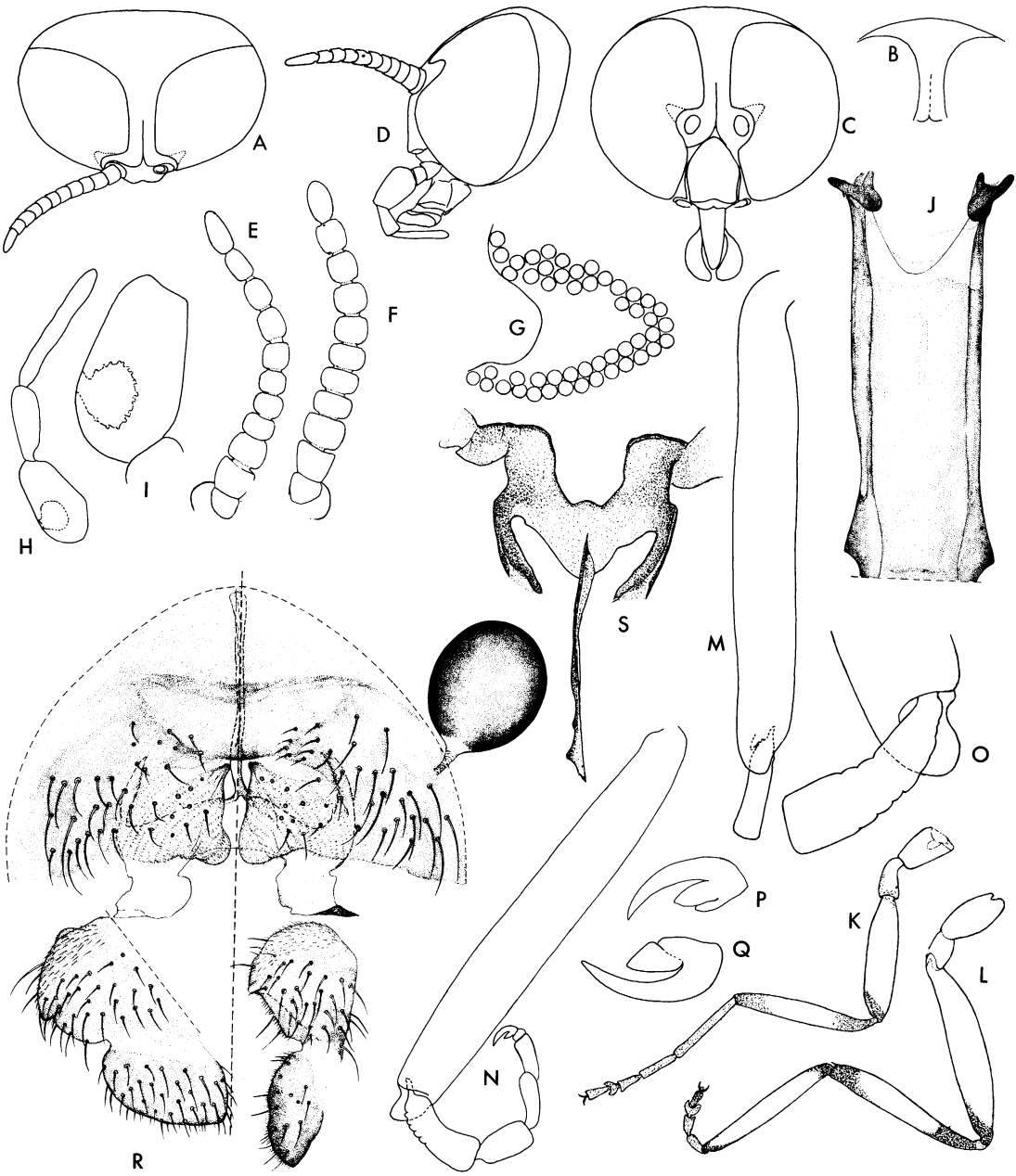

Fig. 37. *Gigantodax brophyi.* Female. **A–D.** Front and head in different views. **E, F.** Antenna. **G.** Fronto-ocular triangle. **H.** Maxillary palp. **I.** Second article of maxillary palp, with sensory vesicle. **J.** Cibarium. **K, L.** Fore and hind leg. **M, N.** Basitarsus of hind leg (N, paratype). **O.** Calcipala, with second tarsal segment. **P, Q.** Claws (P, paratype). **R.** Genitalia in normal position (cercus and paraproct left side in slide position). **S.** Genital fork.

a very short primary branch (fig. 39A–D). Branches in an umbrellalike arrangement, widest at about middle of umbrella-shaped structure. Shape and proportions of clypeus of female and male as shown in figure 39E, F. One pair of short facial trichomes of vari-

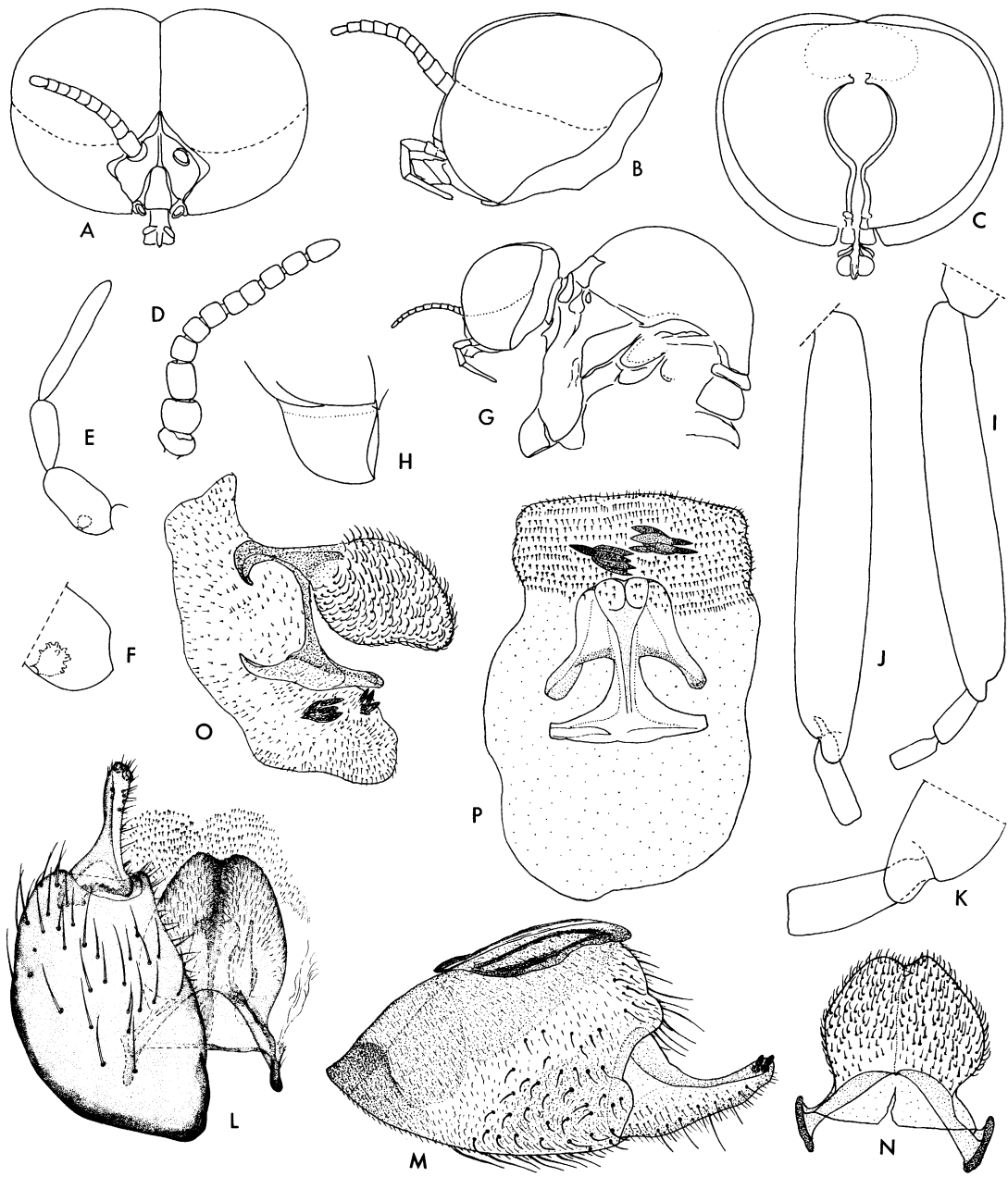

Fig. 38. *G. brophyi.* Male. **A–C.** Head in different positions. **D.** Antenna. **E.** Maxillary palp. **F.** Sensory vesicle of maxillary palp, in situ. (Magallanes). **G.** Head and thorax, side views (paratype). **H.** Katepisternum. **I, J.** Hind basitarsus. **K.** Calcipala with second tarsal segment (type). **L.** Dorsal view of genitalia, showing basimere, distimere, aedaegus, ventral plate, and endoparameral organ. **M.** Basimere and distimere. **N.** Ventral plate. **O.** Aedeagus, ventral plate, and median sclerite, lateral view. **P.** Median sclerite, endoparameral organ and spiculae of aedeagus.

able size present. Frontoclypeus and thorax with smooth platelets, numerous but not forming pattern. Thoracic trichomes not seen. Setae of I and II abdominal tergites slender,

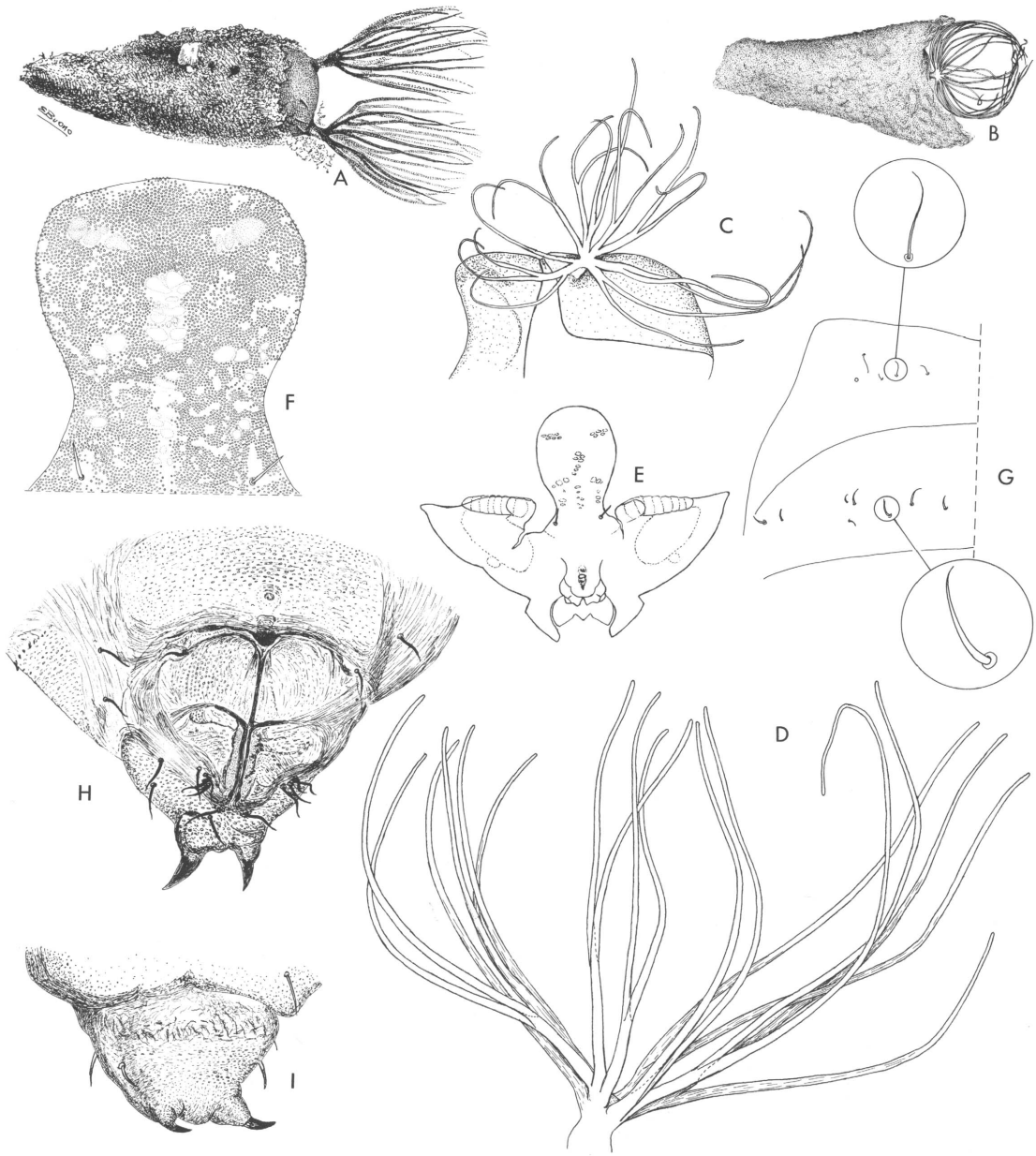

Fig. 39. *G. brophyi.* Pupa. **A, B.** Pupa and cocoon, dorsal and side views. **C.** Anterior portion of body, with gill. **D.** Gill, slide mount. **E.** Frontoclypeus of male. **F.** Frontoclypeus of female with platelets. **G.** Chaetotaxy of abdominal tergites I–II. **H.** Apex of abdomen, ventral aspect. **I.** Apex of abdomen, sublateral view.

about 15 mm long. Tergites III and IV each with 4 + 4 short hooks (fig. 39G). Spinecombs on tergites VI–VIII not interrupted, composed on tergite VII of about 30–35 spines, their length up to 100 μm. Specialized setae of VIII and IX segments irregularly curved and twisted, sternite V with 3 + 3, sternal plates, VI with 2 + 2, II with 1 + 1 hooks. Sternites V–VIII glabrous. Terminal spine as shown in figure 39H, I.

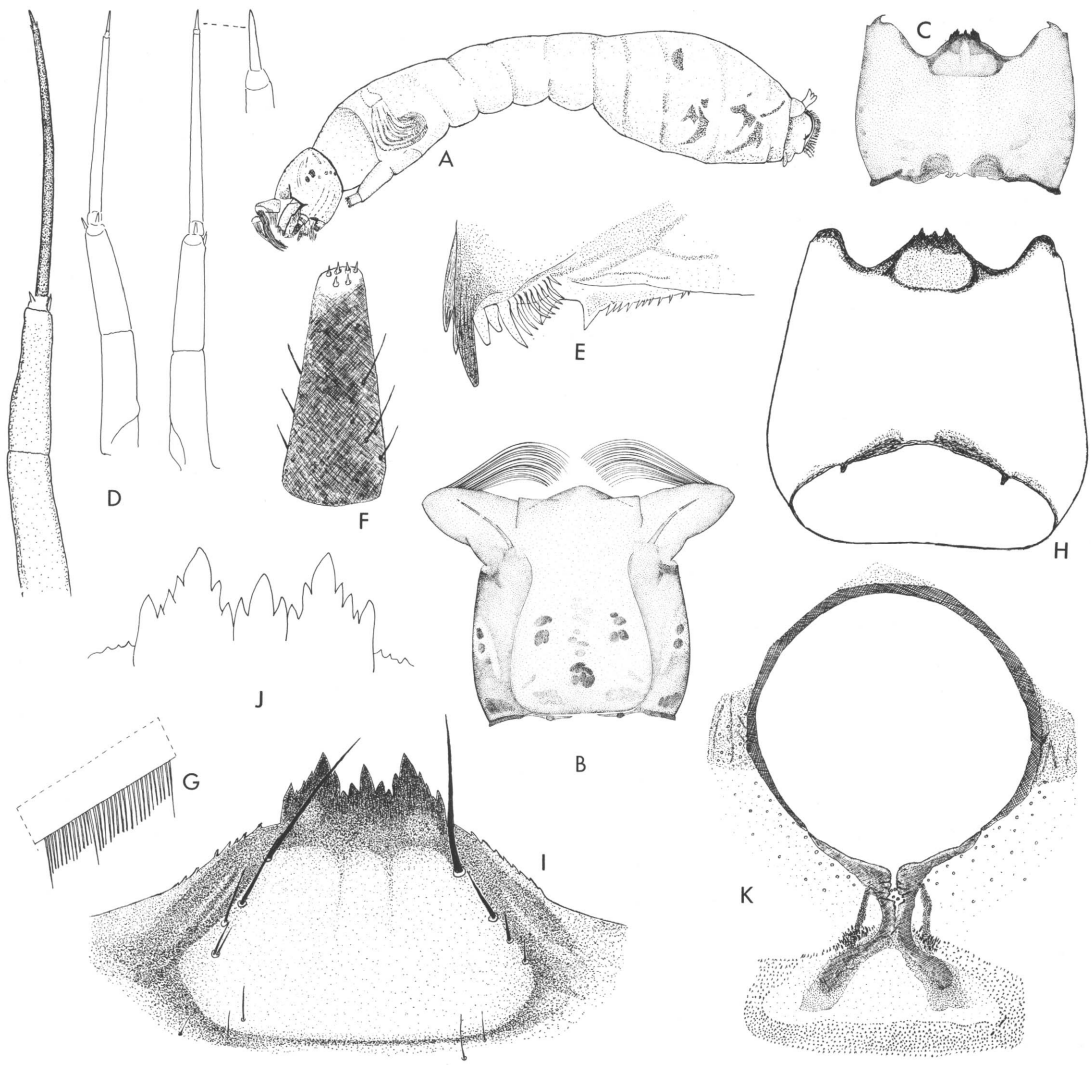

Fig. 40. *G. brophyi.* Larva. **A.** Body, side view. **B.** Head, dorsal view. **C.** Cephalic capsule, ventral view. **D.** Antennae, different positions and magnifications. **E.** Apical portion of mandible. **F.** Maxillary palp. **G.** Teeth of cephalic fan rays. **H.** Cephalic capsule, ventral view in different position than C. **I.** Hypostomium. **J.** Detail of hypostomium teeth. **K.** Anal sclerite.

Mature larva. Body length 8–10 mm. Width of head capsule 0.9 mm. Body shape as shown in figure 40A. Ventral papillae discernible. Color light brown. Head pale yellowish white, with faint darker pattern elements, dorsally as shown in figure 40B. Ventrally as figure 40C, H. Antenna shorter than, or as long as, stem of cephalic fan, light colored, but terminal antennal segment darker than rest. Shape of antenna as illustrated (fig. 40D). Ratio of antennal segments I–III = 1:0.8:1.6–1.9. Terminal sensillum five times as long as wide at base. Cephalic fan consisting of 25–27 large rays, their teeth as shown in figure 40G; small teeth subequal in size. Mandible with 11–12 inner teeth and 12–13 marginal serrations (fig. 40E). Maxillary palpi (fig. 40F) slightly over twice as long as wide at base. Hypostomium as shown in figures 43C, H–J. Median tooth falling distinctly short of level

of apex of fourth lateral tooth. Lines connecting apex of fourth lateral to apex of corner teeth meeting at an angle of 80°. Five or six hypostomial setae in each row. Cervical sclerite very narrow and contiguous, pointed at both ends. Histoblast as in *G. antarcticus.* Perianal scales minute, forming complete perianal ring. Recurrent struts well developed (fig. 40K). Crochet ring with 78–85 rows of 15–20 hooks each.

MATERIAL EXAMINED: ARGENTINA: *Tierra del Fuego:* Ushuaia, Jan. 20–28, 1960 (S. Coscarón and P. Wygodzinsky; AMNH), 5 pupae; Sept. 10, 1983, S. Coscarón; MLP, pupae; near Olivia River, Sept. 10, 1983 (S. Coscarón; MLP), larvae. *Santa Cruz:* Brazo Onelli, Lago Argentino, April 3, 1953 (A. Willink; IML), 1 female. *Chubut:* Rio Pico, Feb. 17, 1961 (S. Coscarón; AMNH), 1 female, 1 male; Lago Fontana, Feb. 15, 1961 (S. Coscarón; MLP), 1 female. *Rio Negro:* Bariloche, Lago Trebol, Nov. 25, 1950 (P. Wygodzinsky; AMNH), 1 female. Lago Nahuel Huapi, Eastern End, Oct. 28–31, 1926 (Edwards; AMNH), paratype; Bariloche, near Rio Manso, Oct. 22, 1970 (S. Coscarón; MLP), 1 male (with pupal exuviae), 3 pupae; 30 km S of Bariloche, Oct. 22, 1970 (S. Coscarón; MLP), 1 pupa; Lago Mascardi, Feb. 3, 1984 (S. Coscarón; MLP), 3 pupae; SW of Pampa Linda road to Tronador, Oct. 22, 1970 (S. Coscarón; MLP), 1 female (with pupal exuviae). *Neuquen:* 30 km NE of Bariloche, s/route 40, Oct. 21, 1970, 1 female (with pupal exuviae) (S. Coscarón; MLP); San Martin de los Andes, Cerro Chapelco (Gentili; MLP) 1700 m, Jan. 1–11, 1983, 2 females, 1400 m, March, 16–24, 1982: 2 females; Apr. 15, 1982, 2 females. CHILE: *Magallanes:* Punta Arenas, 30 m, Nov. 27, 1966 (Irwin-Schlinger; CIS), 1 female; Chorillo Alicia, Feb. 10–20, 1963 (Cekalovic; CNC), numerous larvae, pupae, males and females with their pupal exuviae; Rio Seco, Jan. 3–Feb. 21, 1962, Jan. 4–Feb. 10, 1963 (Cekalovic; CNC), numerous larvae, pupae, and adults with pupal exuviae; Chorrillo Tres Puentes (Cekalovic; CNC), Dec. 3, 1961, larvae and pupae, Sept. 9–Oct. 29, 1962, larvae, Feb. 3, 1 female and 1 male with exuviae, larvae. Chorrillo La Quema, Seno Otway, Feb. 20, 1963 (Cekalovic; CNC), larvae; 8 km NW of Russfin, 300 m, Dec. 1, 1966, dry *Nothofagus* forest (Irwin-Schlinger; CIS), Tres Brazos, Punta Arenas, Nov. 1–3, 1960 (L. Pena; CNC), 6 males; Rio Blanco, land, Jan. 4, 1963 (Cekalovic, CNC), larvae; Cameron, South of Bahia Inutil, Tierra del Fuego, Nov. 14–16, 1960 (L. Pena; AMNH), many males and females. Russfin, 30 km Cameron, Nov. 20–30, 1960 (L. Pena; CNC), 2 males; 10 km N of Punta Arenas, Oct. 31–Nov. 3, 1960 (L. Pena; CNC), 2 males: *Payne* Territory: Cerro Guidobach, Mar. 13, 1958 (Illies), larvae. *Aysen:* Lago Frio, Coilhaique, valley of Rio Simpson, Jan. 20–25 (L. Pena; CNC), 3 females and 1 male.

DISCUSSION: Wygodzinsky has examined the type from Nahuel Huapi, Eastern End, Oct. 28–31, 1926. It has a short calcipala (fig. 37N). The R_1 has only setae; there are no traces of spines. The hind basitarsus ratio is 6.2. The aedeagus membrane has only minute spicules. The male distimere is less than half as long as the basimere. The antennae are annulated as described by Edwards. The "shoulders" of the scutum are light yellow ("indistinctly reddish" in original description), and the dark ring of the hind tibia is slightly subbasal. Abdominal tergites are dark piceous to blackish, with the hind margins of each bordered with whitish. The abdominal fringe is silvery. The wing length is 3.45 mm.

A female paratype was also studied. It has a wing length of 4.2 mm and elongate setae on R_1, but no spines.

Males and females of *G. bonorinorum* are inseparable from those of *G. brophyi.* Small differences in the pupae gills of specimens from Magallanes and Tierra del Fuego, featuring stout and more open branches than specimens from the Bariloche and northern Chubut area, are not sufficient to warrant recognizing two different species. For this reason we recognize the two as synonymous.

Gigantodax rufidulus, new species

Figures 41A–S, 42A–O

DIAGNOSIS: Females and males of this species are close to *brophyi* but the pupae have few platelets on the frontoclypeus and thorax, and the gill branches are more open basally.

Female. Wing length 4.3–4.5 mm. Head blackish, antenna, maxillary palp, clypeus,

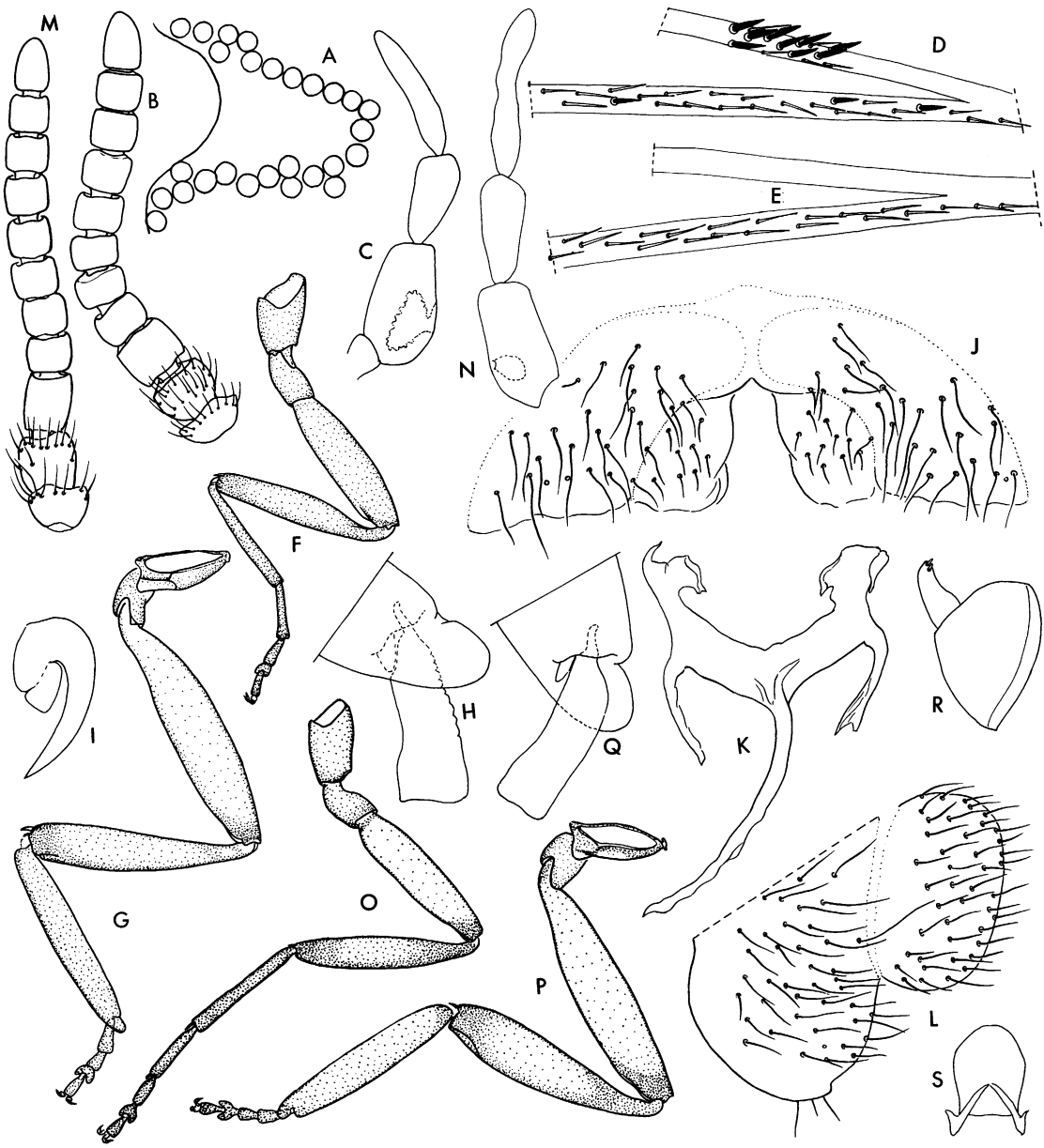

Fig. 41. *Gigantodax rufidulus.* A–L. Female. M–S. Male. **A.** Fronto-ocular triangle. **B.** Antenna. **C.** Maxillary palp. **D, E.** Wing, portions of C and R_1. **F.** Forleg. **G.** Hind leg. **H.** Calcipala, with second tarsal article. **I.** Claw. **J.** Eighth sternite, with gonapophyses. **K.** Genital fork. **L.** Cercus and paraproct. **M.** Antenna. **N.** Maxillary palp. **O.** Foreleg. **P.** Hind leg. **Q.** Calcipala with second tarsal segment. **R.** Basimere and distimere. **S.** Ventral plate.

frons, and occiput grayish brown; basal segment of antenna reddish brown with gray pollinosity. Frons with silver pilosity; hairs of palp and occiput silvery to yellow according to light. Scutum and pleura light reddish brown; scutellum and legs yellowish brown, metanotum reddish brown. Hairs of scutum and scutellum brass to grayish color. Wing

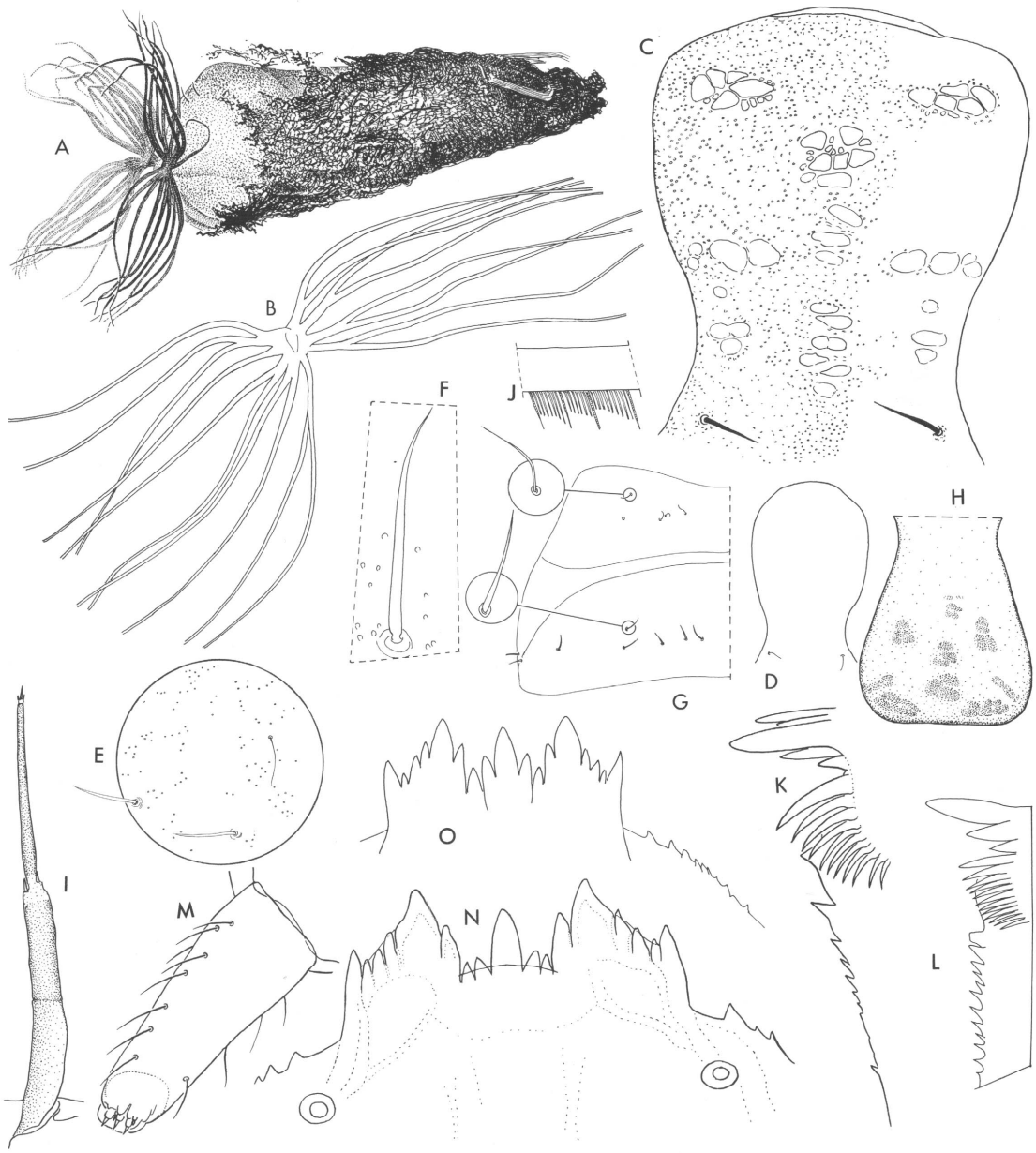

Fig. 42. *G. rufidulus.* A–G. Pupa. **A.** Pupa in cocoon, sublateral view. **B.** Gill, frontal view. **C.** Frontoclypeus of female. **D.** Outline of frontoclypeus of male. **E.** Trichomes of thorax. **F.** Detail of thorax trichome. **G.** Chaetotaxy of abdominal tergites I and II. H–O. Larva. **H.** Cephalic apotome. **I.** Antenna. **J.** Detail of teeth of ray of cephalic fan. **K, L.** Apical portion of mandible. **M.** Maxillary palp. **N, O.** Distal portion of hypostomium.

hyaline with yellowish area between Sc and R_1; veins grayish brown with hairs light to dark brown according to light, spinules dark brown. Halter light brown. Abdomen dark grayish brown, with posterior border of tergites light. Hairs of abdomen as in *antarcticus.*

Frontal angle 55–60°. Fronto-ocular tri-

angle wider than high (fig. 41A). Shape and proportion of antennal segment as in figure 41B. Ratio length/width of second segment of maxillary palp 1:5.5; sensory vesicle wider than half of diameter of basal segment (fig. 41C); mandible with 25 and maxilla with 23 teeth. Structure of sensory vesicle, and hairs of scutum and scutellum as in *antarcticus*. Wing setae in one or two rows, some specimens with spinules (fig. 41D, E). Shape and proportional distribution of pigmentation of segments of fore and hind legs as in figure 41F, G. Ratio length/width of hind basitarsus 4.2. Calcipala longer than wide, slightly longer than half of second tarsomere (fig. 41H). Claw as shown in figure 41I. Plates of abdominal terga as in *antarcticus*. Genitalia as in figure 41J–L. Eighth sternite with homogeneous pigmentation, central and median anterior portion slightly darker.

Male. Wing length 4.4–4.5 mm. Coloration as in female but scutum and pleura slightly darker. Shape and proportion of antennal and palp segments as in figure 41M, N. Structure of sensory organ of palp as in *antarcticus*. Wing chaetotaxy as in female. Shape and distribution of pigmentation of fore and hind legs as in figure 41O, P. Ratio length/width of posterior basitarsus 5.0–5.5. Calcipala about as long as wide and ±0.5 times longer than a half of second tarsomere (fig. 41Q). Genitalia very close to *antarcticus*. Basimere, distimere, and ventral plate as shown in figure 41R, S. Distimere about one-half of basimere length.

Pupa. Irregular cocoon covering most of body, except gills and sometimes anterior portion of thorax (fig. 42A); gills slightly curved forward with intermediate position between *marginalis* and *antarcticus*. Length of body 4.5 mm; cephalopterothecal length 3.0–3.1 mm; length of gill in lateral view 1 mm; in slide each filament about 2.5 mm. Gill filaments with six primary branches as shown in figure 42A, B. Gills dark grayish brown. Structure of gill filaments as in *antarcticus*. Outline of female and male frontoclypeus as in figure 42C, D. Integument of head, thorax, and abdomen light brown, with scarce smooth platelets of different size (fig. 42E); under low magnification, they appear polished. Thorax tricomes as in figure 42F; chaetotaxy of abdominal tergites I–II as shown in figure 42G.

Larva. Maximum length 6.5–7.5 mm; width of cephalic capsule 0.7–0.75 mm. Color of body of larva light gray. Shape as in *antarcticus*; cuticle without hairs, cephalic apotome ornamented as in figure 42H. Antenna slightly shorter than stem of cephalic fan. Antenna as in figure 42I, proportion of segments I–III = 1:0.9:1.5. Terminal sensillum 4–5 times as long as wide at base. Maxillary palp 2.5 times as long as wide (fig. 42M). Cephalic fan with about 30–35 rays; detail of tooth ray as in figure 42J. Mandibular dentition as in figure 42K, L, with 11–12 internal teeth, with 10–12 marginal serrations. Ratio length/width at base of maxillary palp = 3.0. General aspect of hypostomium very close to *antarcticus*; median tooth shorter than corner teeth (fig. 42N, O). Proleg sclerite with about 48 teeth. Crochets ring with 95 rows of 18–20 hooks each.

HOLOTYPE: ARGENTINA: *Neuquen:* 5 km N Lago Nahuel Huapi on Highway q, October 23, 1970 (S. Coscarón; MLP), male.

PARATYPES AND ADDITIONAL SPECIMENS: ARGENTINA: *Tierra del Fuego:* Tierra Mayor, Jan. 25, 1960 (Wygodzinsky and Coscarón; MLP), 1 female (with pupal exuviae); *Santa Cruz:* Rio Turbio, Jan. 19, 1960 (Bachmann and Del Ponte; MLP), 1 pupa. *Chubut:* Lago Fontana, Feb. 3, 1961 (S. Coscarón; MLP), 1 pupa. *Rio Negro:* Bariloche, Nov. 23, 1950 (P. Wygodzinsky; AMNH), 3 females, 1 male (with pupal exuviae), paratypes; same, Nov. 27, 1950 (P. Wygodzinsky; AMNH), 7 females, 2 males (with pupal exuviae), pupae, and larvae; Cerro Catedral, 1000 m (P. Wygodzinsky; AMNH), 1 female, 1 male, paratypes, 1 intersex (with pupal exuviae), pupae, and larvae; Bariloche, Oct. 1970 (S. Coscarón; MLP), 1 female; Cerro Catedral, Arroyo La Cascada, Oct. 23, 1970 (S. Coscarón; MLP), 1 pupa; Bariloche, Sept. 27, 1975 (S. Coscarón; MLP), 1 female (with pupal exuviae), pupae; Bariloche, 5 km NE of city, Oct. 23, 1970 (S. Coscarón; MLP), pupae; 4 km E of Pampa Linda, 850 m, road to Tronador, Oct. 22, 1970 (S. Coscarón; MLP), 2 females (with pupal exuviae), paratypes, pupae; Valle de los Vuriloches, small creek near Rio Manso, road at Tronador, Oct.

22, 1970 (S. Coscarón; MLP), 1 female (with pupal exuviae), pupae; Colonia Suiza, June 26, 1983 (S. Coscarón; MLP), 1 pupa; base of Cerro Lopez, Sept. 27, 1975 (S. Coscarón; MLP), 1 female (with pupal exuviae). *Neuquen:* same data as holotype, female allotype, 1 female, 7 male paratypes (with pupal exuviae), in AMNH, 3 females, 3 male paratypes, pupae; same, Sept. 25, 1975, 2 females (with pupal exuviae), pupae; Valle Encantado, Oct. 21, 1970 (S. Coscarón; MLP), pupae; 30 km NE of Bariloche, Oct. 22, 1970 (S. Coscarón; MLP), 1 male (with pupal exuviae), pupae; 5 km S of La Lipela, Sept. 25, 1975 (S. Coscarón; MLP), 1 male (with pupal exuviae), pupae; Confluencia, Oct. 25, 1970 (S. Coscarón; MLP), pupae; 10 km SE of San Martin de los Andes, 960 m, Oct. 23, 1970 (S. Coscarón; MLP), 4 females, 2 males (with pupal exuviae) paratypes, pupae; San Martin de los Andes (at light) (M. Gentili; MLP), March 16, 1982, 8 females, 2 males; April 5–15, 1982, 13 females, 1 male; Cerro Chapelco, 1650 m (at light), Jan. 11, 1983 (M. Gentili; MLP), 7 females; same, 1400 m, Jan. 1, 1983, 1 female, Oct. 5, 1983, 1 female; Rio Chapelco Chico; Oct. 20, 1970 (S. Coscarón; MLP), 2 males (with pupal exuviae), pupae; Piedra del Aguila, Sept. 28, 1975 (S. Coscarón; MLP), 1 male (with pupal exuviae) pupae. CHILE: *Magallanes:* Punta Arenas, Tres Brazos, Nov. 1–3, 1960 (L. Pena; CNC), 1 female; Punta Arenas, Chorrillo Tres Puentes, Dec. 3, 1961 (Cekalovic; CNC), 1 pupa.

ETYMOLOGY: Referring to the reddish color in the antenna, scutum, and pleura.

BIOLOGY: *Gigantodax rufidulus* breeds in small creeks with clear flowing waters. It was collected together with *S. antarcticus, G. marginalis,* and *Cnesia ornata.* It is sometimes parasitized by mermithids. A few intersex specimens were found.

DISCUSSION: Imagos are very difficult to separate from *brophyi* and *antarcticus.* Coloration is similar to *brophyi,* and *antarcticus* has scutum only slightly darker. The calcipala is shorter in *antarcticus* and *brophyi,* but in *rufidulus* it is possible to find specimens with the calcipala shorter than half of the second tarsomere; also in *rufidulus* the wings do not have spinules on R_1. The best character for differentiating these closely related species is in the pupa: *G. rufidulus* has small and sparse platelets on the frontoclypeus and thorax, perceptible only with high magnification in slide-mounted specimens. *Gigantodax marginalis* pupae also have sparse platelets, but the gills in dry material appear blackish; also the size is smaller in *marginalis.* The female of *G. femineus* is smaller and with lighter coloration, orange in tone, and the pupa, as in *antarcticus* and *brophyi,* has more platelets.

Gigantodax antarcticus (Bigot)

Figures 43A–Z, AA–DD, 44A–S, 45A–K, 46A–L

Simulium antarcticum Bigot, 1888: 15. Pinto, 1931: 671.

Simulium (*Gigantodax*) *antarcticum:* Edwards, 1931: 132. Orfila, 1935: 1527. Smart, 1945: 499.

Simulium (*Gigantodax*) *nigrescens* Edwards, 1931: 133. NEW SYNONYMY.

Gigantodax antarcticum: Wygodzinsky, 1961a: 460; 1961b: 563. Vulcano, 1967: 2; 1977: 290. [Incorrect gender]

DIAGNOSIS: Imagos without spinules on R_1 and calcipala shorter than half the length of second tarsomere, pupal gill with 8 dorsal and 10 ventral branches disposed in two closely spaced bundles, in shape of an incomplete circle.

REDESCRIPTION: *Female.* Wing length 4.0–4.7 mm. Head dark. Antenna, palp, clypeus, frons, and occiput grayish brown; scapus and pedicellus light brown; frons and clypeus pollinose; hairs of antenna very short, silvery, those of palp, frons, clypeus, and occiput longer and from silvery to light brown. Scutum, scutellum, and pleuron from light to dark reddish brown and with grayish pollinosity; postnotal areas lighter colored. Scutum with dense, decumbent, brass-colored setae, obscuring in well-preserved specimens the median and 1 + 1 lateral grayish lines of scutum; in well-preserved specimens scutum appearing brass colored due to color of setae. Setae of scutellum from yellow to brown. Metanotum reddish brown, slightly darker than scutum, and with grayish pollinosity. Pleural tuft from pale gray to light brown. Wing hyaline, veins light brown; hairs at base of wing from grayish to pale brown; hair and spines on veins from dark brown to black.

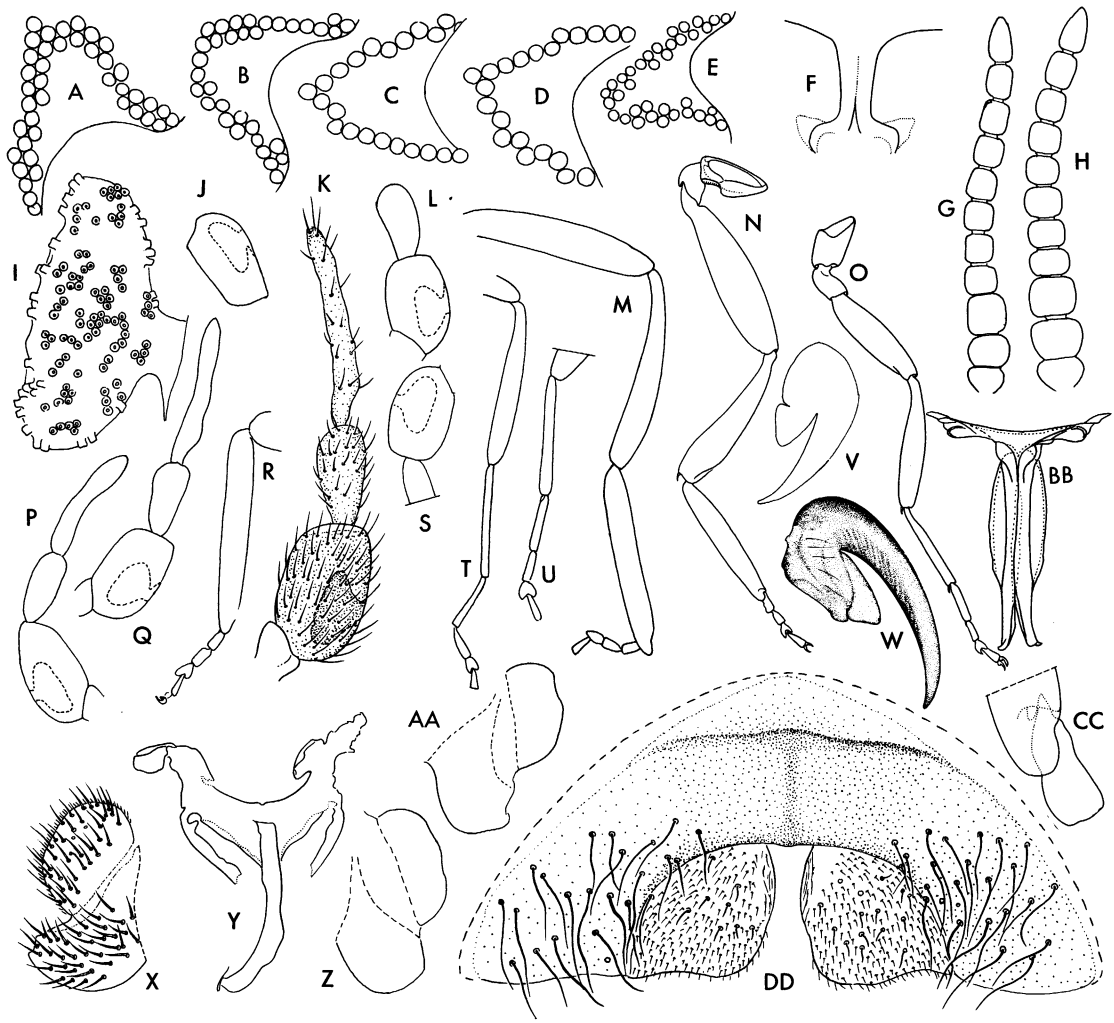

Fig. 43. *G. antarcticus.* Female. **A–E.** Fronto-ocular triangle in different localities (A. Puerto Limonao, B. Rio Turbio, C. Lago Gutierrez, D. Rio Turbio, E. El Canelo). **F.** Frons. **G, H.** Antennae (G. Futalaufquen, H. Rio Turbio). **I.** Sensory vesicle of maxillary palp. **J.** Second article of maxillary palp (Puerto Limonao). **K.** Maxillary palp. **L.** Portion of maxillary palp, wtih sensory organ (Rio Turbio). **M, N.** Hind leg (M. Puerto Limonao, N. Rio Turbio). **O.** Foreleg. **P, Q.** Maxillary palp, wtih sensory organ (P. Puerto Limonao. Q. Rio Turbio). **R.** Posterior tarsus. **S.** Second article of maxillary palp. **T.** Foreleg, Futalaufquen. **U.** Portion of foreleg (Rio Turbio). **V, W.** Claws of female, different magnification. **X.** Cercus and paraproct (El Canelo). **Y.** Genital fork. **Z.** Cercus and paraproct (Rio Turbio). **AA.** Cercus and paraproct (Puerto Limonao). **BB.** Furcasternum. **CC.** Calcipala female (Rio Turbio). **DD.** Eighth sternite with gonapophyses.

Halter and legs light brown, joints and tarsi somewhat darkened. Hairs of legs from pale gray or golden to light brown. Abdomen dark grayish brown, with posterior portion of terga lighter. Basal fringe with very long brass-colored hairs; remaining setae of abdomen shorter, from brass colored to dark brown.

Frons with medium sulcus as shown in figure 43F. Fronto-ocular triangle (fig. 43A–E) wider than deep. Shape and ratios of articles of antenna as shown in fig. 43G, H. Terminal article of maxillary palp over twice as long as penultimate and slightly shorter than the two preceding combined (fig. 43K, P, Q). Sec-

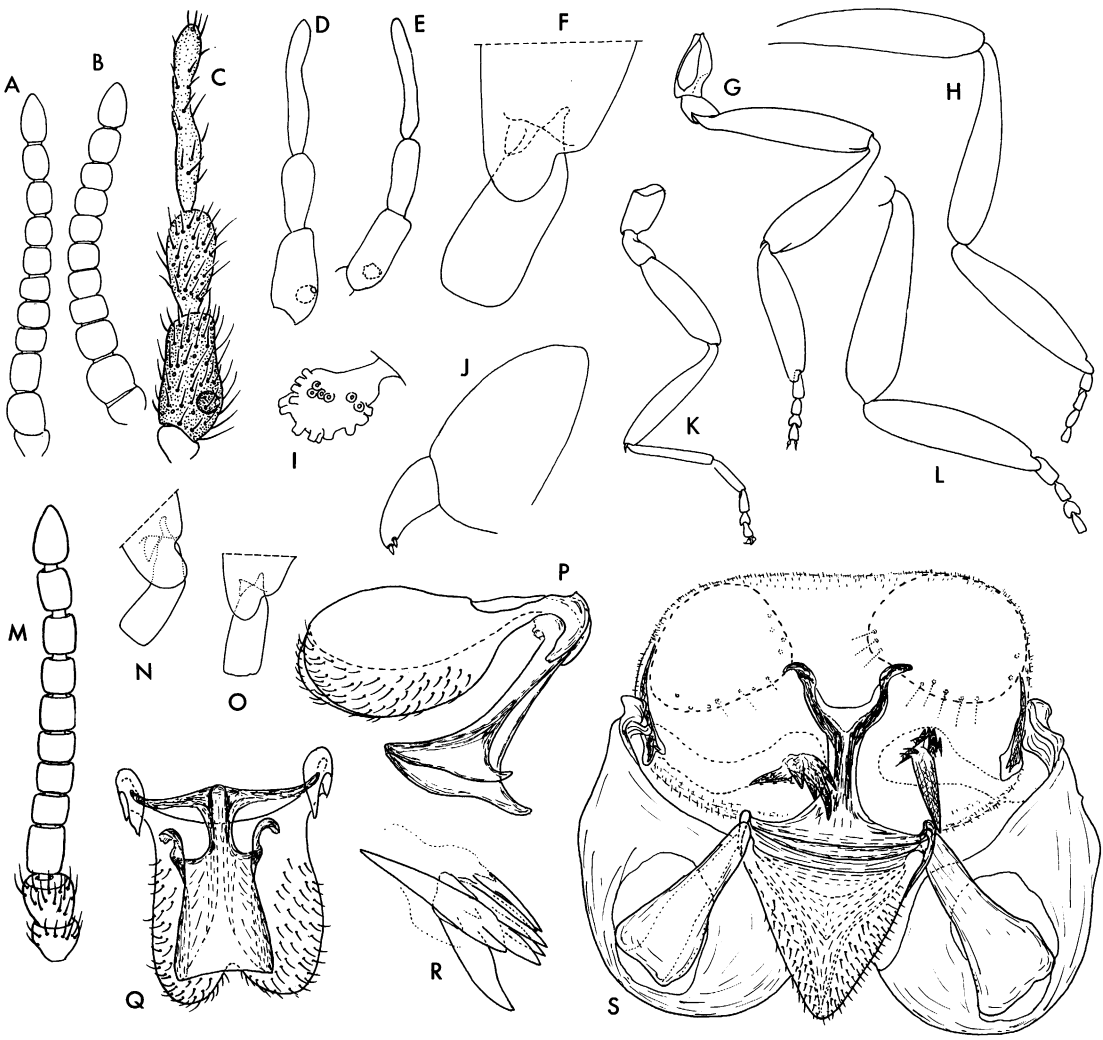

Fig. 44. *G. antarcticus.* Male. **A, B.** Antennae (A. Futalaufquen. B. Rio Turbio). **C–E,** maxillary palp (C, D. Rio Turbio, E. Futalaufquen). **F.** Calcipala, with second tarsal segment. **G, H, L.** Hind legs (G. Rio Turbio, H. Futralaufquen, L. Rio Turbio). **I.** Sensory organ of maxillary palp. **J.** Basimere and distimere. **K.** Forleg. **M.** Antenna. **N, O.** Calcipala with second tarsal segment (N. Futalaufquen. O. Rio Turbio). **P.** Median sclerite, lateral view. **Q.** Ventral plate. **R.** Endoparameral organ. **S.** Genitalia, total aspect.

ond segment very wide, ratio length/width = 1:0.58–0.66 with sensory vesicle approximately half as wide as article (fig. 43J, L, S); structural detail of vesicle as shown in fig. 43I. Maxilla with 27–30 teeth; mandible with 22–25 teeth on one edge only. Wing with spines on C appearing on posterior four-fifths of length of vein; Sc with simple hairs. Basal portion of R with hairs arranged in two to three rows, similarly arranged hairs on R_1, spines of R_1 absent; R_s with hairs arranged in one to three series on undersurface of wing, on upper surface with one row of hairs beginning approximately at base of second half of vein. Furcasternum as shown in figure 43BB. Shape and ratio of leg segments as shown in figure 43M, N, O, R, T, U. Calcipala longer than wide, not reaching level of center of second tarsomere (fig. 43CC). Claw as shown in figure 43V, W. Abdominal tergites

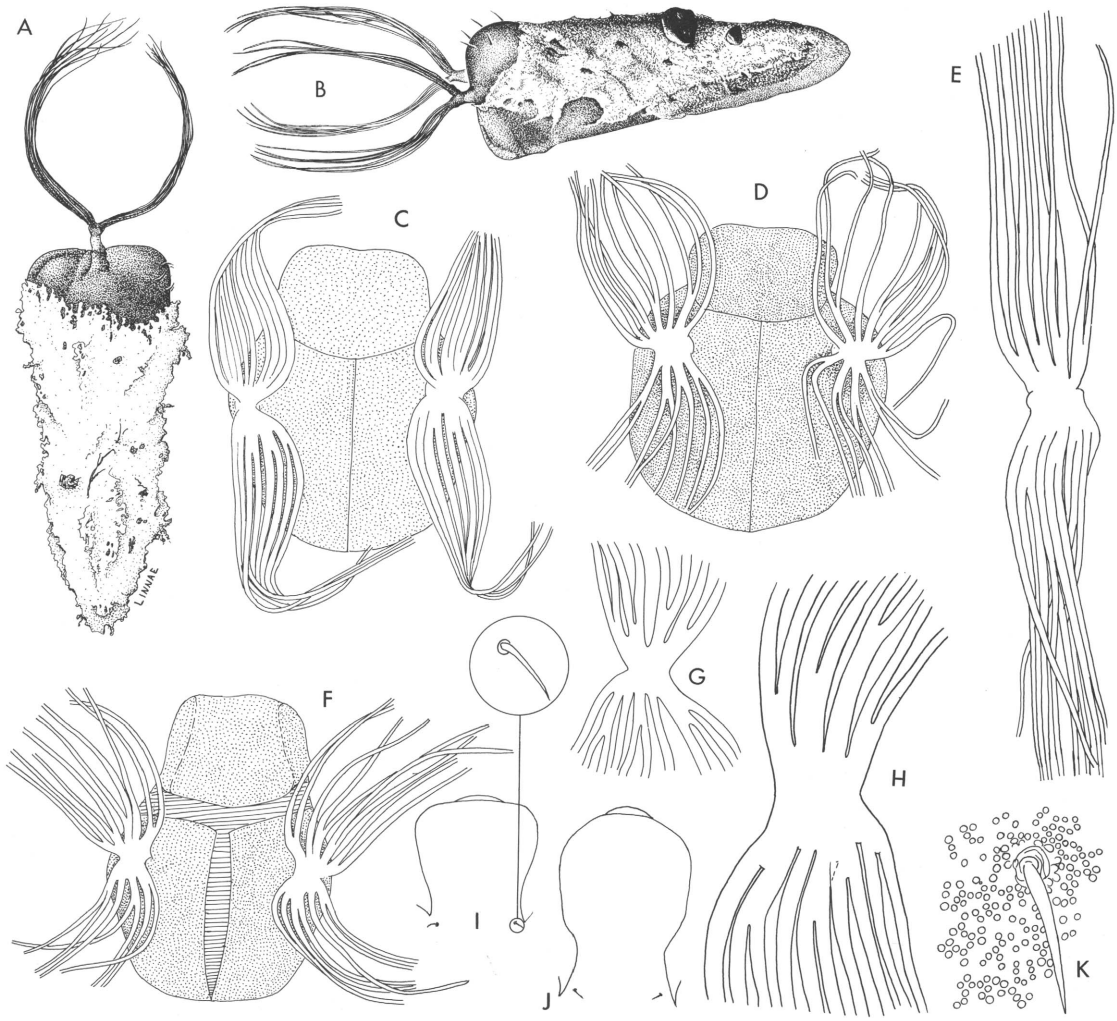

Fig. 45. *G. antarcticus.* Pupa. A, B. Pupa in cocoon, general aspect. **A.** Lateral view. **B.** Dorsolateral view. **C, D, F.** Gills, frontal view (**C.** Pucara, Neuquen, **D, F.** Rio Turbio). **E.** Gill, Futalaufquen. **G, H.** Base of gills (G. El Canelo, H. Futalaufquen). **I, J.** Frontoclypeus of female and male. **I.** Outline of frontoclypeus, female. **J.** Outline of male frontoclypeus. **K.** Seta of thorax with platelets.

weakly sclerotized and not well defined, much as in *rufidulus.* Eighth sternite with 1 + 1 groups of approximately 25 strong setae each; pigmentation as shown in figure 43DD. Gonapophyses subquadrate, membranous, internal borders somewhat more sclerotized, with microtrichia and each with 8–14 setae. Paraprocts subtriangular with distal portion rounded; cercus wide (fig. 43X, Z, AA). Genital fork with stem well sclerotized, with lateral projections distinct, anterior projections wide (fig. 43Y). Spermatheca oval, neck not sclerotized, spinules distinct.

Male. Wing length 3.9–4.0 mm. Head blackish. Eyes dark brown in area of large ommatidia and black in area of small ones. Antenna, maxillary palp, and clypeus from light brown to dark grayish brown, clypeus silvery pollinose. Antenna with short hairs, longest on scapus and pedicellus. Setae of occiput, interocular space, clypeus, and basal segments of palp from yellowish gray to

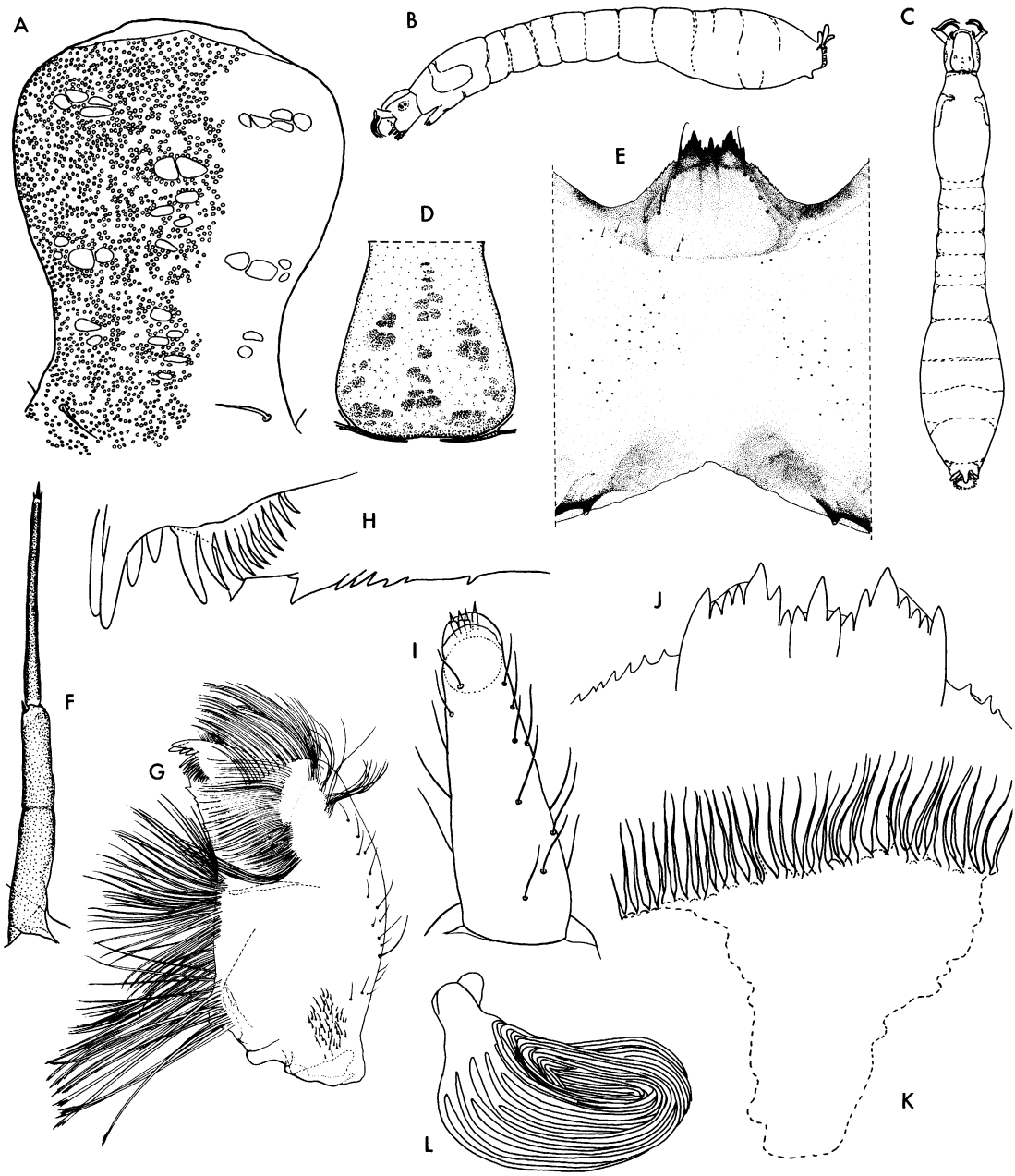

Fig. 46. *G. antarcticus.* **A.** Pupa, frontoclypeus, female. B–K. Larva. **B, C.** Larvae, lateral and dorsal view. **D.** Cephalic aptome, dorsal view. **E.** Hypostomium and hypostomial bridge. **F.** Antenna. **G.** Mandible. **H.** Apex of mandible. **I.** Maxillary palp. **J.** Hypostomial teeth and lateral serrations. **K.** Lateral sclerite of proleg. **L.** Gill histoblast.

brown. Thorax brown; scutum from reddish brown to piceous, with pronotal and lateral portions lighter colored when setae rubbed off; scutellum pale brown, metanotum dark brown, silvery pollinose. Hairs of metanotum numerous, from brass colored to golden; hairs of scutellum golden. Pleura light brown, silvery pollinose. Wing, halter, and legs col-

ored as in female, but legs darker and with darker and longer hairs. Abdomen dorsally from dark brown to black, pale gray along hind border of terga. First abdominal segment brown, with long pale silvery yellow hairs, remaining abdominal hairs of identical color, shorter. Sides and undersurface of abdomen pale grayish brown. Shape and ratios of antennal segments as shown in figure 45A, B, M. Apical segment of maxillary palp approximately twice as long as penultimate (fig. 44C–E). Diameter of palp sensory vesicle less than half as long as diameter of segment, its structure as shown in figure 44I. Wing as in female (in some specimens spines on C beginning closer to base of vein). Shape and proportions of leg segments as shown in figure 44G, H, K, L. Calcipala approximately as long as wide, not attaining level of middle of second tarsal segment (fig. 44F, N, O). Posterior basitarsus 4.2–5.0 times as long as wide. Dorsal plates as in female. Genitalia much as illustrated for *brophyi.* Basimere subtriangular, distimere narrowed, with one or two apical spines (fig. 44J, S). Median sclerite as shown in figure 44P, Q, S, basal portion wide but not deep, with a median branch arising from it which bears the distal plate, the latter with two appendages on its anterior border and with the posterior border almost straight. Endoparameral organ membranous, with one large and several small apical spines (fig. 44R). Membrane of aedeagus as in *brophyi.*

Pupa. Cocoon of irregular shape, covering almost entire body of pupa except anterior portion of thorax dorsally and gills (fig. 45A, B). Cocoon light brown, of irregular texture, not very dense, mesh perceptible; sand grains of various sizes often incorporated into cocoon. In some specimens, outline of pupa visible through cocoon. Length of body of pupa 4.7–5.5 mm; cephalopterothecal distance 3.1–3.3 mm. Length of gill filaments 4.7–5.5 mm; their color dark grayish brown. Filaments arranged in two closely spaced bundles, laterally, in shape of an incomplete circle (fig. 45A, B), with eight dorsal and ten ventral. Primary branches arising from a short basal trunk, both branches subdividing at a very short distance from their origin (fig. 45C–H). Dorsal branch forming four secondary branches, the two internal and the extreme external branches subdivided at a short distance, the remaining branch subdivided at a larger distance. Ventral primary branch divided almost at its base into five secondary branches which again subdivide except the second internal branch which remains simple; outer branch of the second internal subdivided into two filaments. Filaments gradually narrow towards apex. Microstructure of filaments much as illustrated for *brophyi* Head and thorax of pupa light colored, covered by somewhat darker, glabrous platelets. Distribution of platelets on clypeus as illustrated (fig. 46A). Outline of male fontoclypeus as figure 45I, J. Platelets of thorax large and distinct on anterior dorsal portion of thorax which is normally exposed; smaller, and less strongly sclerotized on rest of thorax. Setae of thorax much as in *brophyi,* viz., with three large dorsocentral spines and from three to six smaller setae; all situated on exposed portion of thorax. Platelets and onchotaxy of abdomen as in *brophyi.*

Larva. Length of mature larva 9.0–9.7 mm; width of head 0.8 mm. Body shape as shown in figure 46B, C. General color pale brownish gray. Cephalic apotome with pattern as shown in figure 46D. Hypostomial bridge pigmented homogeneously (fig. 46E). Antenna a little shorter than stem of cephalic fan. Antenna light brown; third segment very long, almost as long as first and second combined (fig. 46F). Ratios of segments I–III: 1:0.8–0.9:1.8–1.9. Terminal sensillum four times as long as wide at base. Large cephalic fan with 34–40 rays. General aspect of mandible as shown in figure 46G. Mandibular teeth as illustrated (fig. 46H), with 11–12 internal teeth and 7–9 mandibular serrations. Maxillary palp as shown in figure 46I. Hypostomium as shown in figure 46J. Median tooth below level of corner teeth, the external being the largest of the intermediate teeth; lateral teeth decreasing in size toward side of hypostomium except the outermost tooth, which is the largest. Hypostomial setae numbering from four to six, arranged in one or two irregular series; disc with three to four setae. Cervical sclerite discontinuous. Lateral sclerite of proleg as shown in figure 46K. Histoblast as illustrated (fig. 46L). Anal sclerite as in *brophyi,* with scales at base and long setae near ring. Re-

current struts well pigmented. Crochet ring with 115–125 rows, each composed of 19–21 hooks.

MATERIAL EXAMINED: ARGENTINA: *Tierra del Fuego:* Ushuaia, Laguna Escondida, Jan. 20, 1960 (S. Coscarón; MLP), 1 male (reared, with associated pupal exuviae). *Santa Cruz:* Rio Turbio, Jan. 17, 1960 (P. Wygodzinsky; AMNH), pupae; Rio Turbio, Jan 19, 1960 (A. Bachmann; MLP), 5 males, 1 female (reared, and with associated pupal exuviae), pupae and larvae; Lago Argentino, Brazo Onelli, March 1953 (A. Willink; IML), 3 females; Lago Argentino, March, 1953 (A. Willink; IML), 2 females; Lago Argentino, Jan. 9–10, 1961 (L. Pena; CNC), 1 female. *Chubut:* Lago Futalaufquen, near Hosteria, Jan. 12, 1962 (S. Coscarón; MLP), 5 males, 2 females (all reared, and with associated pupal exuviae), pupae and larvae; Puerto Limonao, Jan. 14, 1962 (S. Coscarón; MLP), 1 male, 1 female, pupae and larvae; Laguna Blanca, Feb. 8, 1961 (S. Coscarón; MLP), 1 female (reared, and with associated pupal exuviae), pupae; Lago Vintter, Feb. 18, 1961 (S. Coscarón; MLP), pupa. *Rio Negro:* Bariloche, Dec. 1, 1926 (Shannon, det. Edwards; USNM), 1 male; Bariloche, Nov. 25, 1950 (P. Wygodzinsky; AMNH), pupa; Bariloche, Arroyo Michay, Jan. 22, 1971 (S. Coscarón; MLP), pupae; Bariloche, Colonia Suiza, Sept. 27, 1975 (S. Coscarón; MLP), pupa; Arroyo Pilmaiquen, Jan. 28, 1971 (S. Coscarón; MLP), pupae; small stream above Lago Gutierrez, Jan. 23, 1971 (S. Coscarón; MLP), pupae; Lago Guiterrez, Feb. 17, 1967 (S. Coscarón; AMNH), pupa; Lago Gutierrez, Nov. 3–14, 1926 (Shannon; AMNH), 1 female paratype det. Edwards of *nigrescens*; Bariloche, Nov. 1–Dec., 1926 (Shannon; USNM), 1 female paratype of *nigrescens* det. Edwards; Nahuel Huapi, Eastern End, Oct. 28–31, 1926 (Shannon, AMNH), 1 male paratype of *nigrescens,* det. Edwards; Rio Foyel, Nov. 29, 1950 (P. Wygodzinsky; AMNH), 1 male (reared, and with associated pupal exuviae), pupae; Lago Mascardi, Feb. 15, 1967 (S. Coscarón; AMNH), 1 female (reared, and with associated pupal exuviae), pupae; Arroyo La Cascada, base of Cerro Catedral, Jan. 22, 1971, several larvae; small stream near Ayo. La Virgen, road to Bahia Lopez, Jan. 23, 1971, several larvae; Arroyo Michay, Bariloche, Jan. 23, 1971, pupae and larvae; Arroyo Lopez, base of Cerro Lopez, road to Bahia Lopez, Jan. 23, 1971, larvae; Arroyo Pilmayquen, Lago Gutierrez, Jan. 24, 1971, pupae and larvae; Lago Gutierrez small stream on road to El Bolson, 24-I-71, pupae and larvae. *Neuquen:* 30 km NE of Bariloche, Oct. 22, 1970 (S. Coscarón; MLP), 3 females (reared, and with associated pupal exuviae), pupae; Valle Encantado, on road 40, Oct. 21, 1970 (S. Coscarón; MLP), pupa; Arroyo Mulahuanca, 15 km N Confluencia, on road 40, Oct. 24, 1970 (S. Coscarón; MLP), pupae; Pucara, Parque Lanin, Nov. 1954 (S. Schajovskoy, IML), 1 female; Pucara, Parque Lanin, San Martin de los Andes, Ayo. Quiltrahue, Dec. 21, 1980, Gentili (MLP), 1 pupa; Feb. 20, 1967 (S. Coscarón; AMNH), pupa. CHILE: *Magallanes:* Punta Arenas, Tres Brazos, Nov. 1–3, 1960 (L. Pena; CNC), 2 female pupae; Punta Arenas, Chorrillo Tres Puntas, Nov. 29, 1961 (Cekalovic; CNC), pupa; Tierra del Fuego, 60 km of Punta Arenas, Dec. 10, 1960 (L. Pena; CNC), 1 male; Tierra del Fuego, Jan. 5, 1933 (J. Bird; CNC), 1 male; 30 km S El Porvenir, N of Bahia Inutil, Dec. 6–7, 1960 (L. Pena; CNC), 1 male; Isla Desolacion, Oct. 4, 1969 (O. Flint; USNM), 1 male, 2 females. *Aysen:* Puerto Cisnes, Feb. 16–18, 1961 (L. Pena; CNC), 1 female; 30 km N of Puerto Ibanez, Jan. 7, 1961.

BIOLOGY: The aquatic instars of this species are normally found in very small slow-flowing streams, located on stones or on leaves of aquatic plants. The pupae are frequently covered with grains of sand which makes them difficult to detect. According to Cekalovic (label data) the stream temperatures where pupae were found were 3°C in November and 10°C in December. In Lago Mascardi, the species was collected with *G. chilensis.*

DISCUSSION: We have examined the type of *antarcticus,* in the Museum National d'Histoire Naturelle, Paris, and also the male holotype of *G. nigrescens,* in the British Museum (Nat. Hist.), together with two female paratypes. All of these specimens agree fully with our morphological interpretation of *antarcticus,* thus the new synonymy.

The adults of this species are quite homogeneous morphologically, but the inten-

sity of their pigmentation varies considerably, which caused Edwards to place very dark specimens in a different species (*nigrescens*).

This species is very close to *trifidus,* differing only in the pupal gills, which are in three bundles and more open in side view. It is also very close to *brophyi* and *rufidulus*; females of this species are almost indistinguishable, and males are distinguishable only by the gill branches being in an umbrellalike arrangement in *brophyi,* but dorsally flattened in *rufidulus.*

Gigantodax trifidus, new species
Figures 47A–R; 48A–M

DIAGNOSIS: Female and male of this species are distinguishable from *antarcticus* only by small differences as shown in the discussion; the pupal gill arranged in three bundles is the differentiating character.

DESCRIPTION: *Female.* Wing length 3.7–4.2 mm; head coloration as in *antarcticus* but antenna lighter yellowish brown with silky yellow hairs. Scutum, scutellum reddish brown with hairs silver to brass colored, pleura light grayish with dark gray pollinosity; metanotum grayish brown, with dark grayish pollinosity. Wing, legs, and abdomen as in *antarcticus.* Frons shape as in *antarcticus*; fronto-ocular triangle wider than high (fig. 47B). Shape and ratio of articles of antenna and maxillary palp as shown in figure 47A, C, respectively. Ratio length/width of second segment of maxillary palp = 1:0.5 (fig. 47C). Structural detail of vesicle as shown in figure 47H. Maxilla with 18–36 teeth and mandible with 21–28 teeth. Chaetotaxy of wings as in *antarcticus.* Shape and ratio of fore and hind leg segments as shown in figure 47D, E. Calcipala longer than wide (fig. 47F), shorter than half of length of tarsomere 2. Basal process of claw as in figure 47K. Tergal plates of abdomen and eighth sternite and gonapophyses very close to those of *antarcticus.* Paraproct, cercus, and genital fork as in figure 47I, G, respectively. Spermatheca as in *antarcticus.*

Male. Wing length 3.5–3.8 mm. Eye reddish brown in area of large ommatidia, and blackish on area of small ones. Antenna yellow brown with yellowish hairs, maxillary palp and clypeus light brown. Antenna with short hairs, somewhat longer on scapus and pedicullus; seta of occiput, clypeus, and basal segment of maxillary palp from yellowish gray to brown. Thorax brown, scutum, scutellum light brown piceous; metanotum dark brown, silvery and pollinose, hairs of metanotum numerous, from brass colored to golden, hairs of scutellum light brown. Pleura light brown, silvery, and pollinose; wing halter and legs colored as in female. Abdomen dorsally brown to piceous, pale gray to yellowish on the hind border of terga at sides; ventrally brownish gray.

Shape and ratios of antennal segments as shown in figure 47L. Apical segment of maxillary palp approximately twice as long as penultimate (fig. 47P). Diameter of sensory vesicle less than half as long as diameter of segment; structure as in figure 47O. Wing as in female. Shape and proportions of fore and hind leg segments as in figure 47M, N. Calcipala longer than wide, shorter than half of second tarsal segment (fig. 47J). Posterior basitarsus 5.5–5.9 times as long as wide. Dorsal plates as in female. Genitalic morphology very close to that of *antarcticus*; basimere and distimere as in figure 47R; distimere with one apical spine. Ventral plate as shown in figure 47Q.

Pupa. Cocoon shape as in figure 48A, in most specimens, outline of pupa visible through cocoon. Length of pupal body 3.7–4.3 mm. Cephalopterothecal distance 2.7–3.1 mm. Length of gill filaments 2.3–2.7 mm, their color light brown. Gill filaments arranged in three closely spaced bundles (fig. 48C, D, G), one dorsal and two ventral in frontal view, in shape of an incomplete circle in lateral view. Gill filaments are disposed eight dorsally, six ventral (externally), and four (ventral) inwardly (sometimes the dorsal group is subdivided in two groups and shows four bundles). Primary branches arising from a short basal trunk, both subdividing at very short distance from their origin. Dorsal primary branch has four secondary branches that are subdivided very close to the base, forming eight tertiary branches. Ventral external primary branch has three secondary branches that are subdivided, each very close to the base, into two branches, giving in total six tertiary branches. The ventral internal primary branch forms three secondary branch-

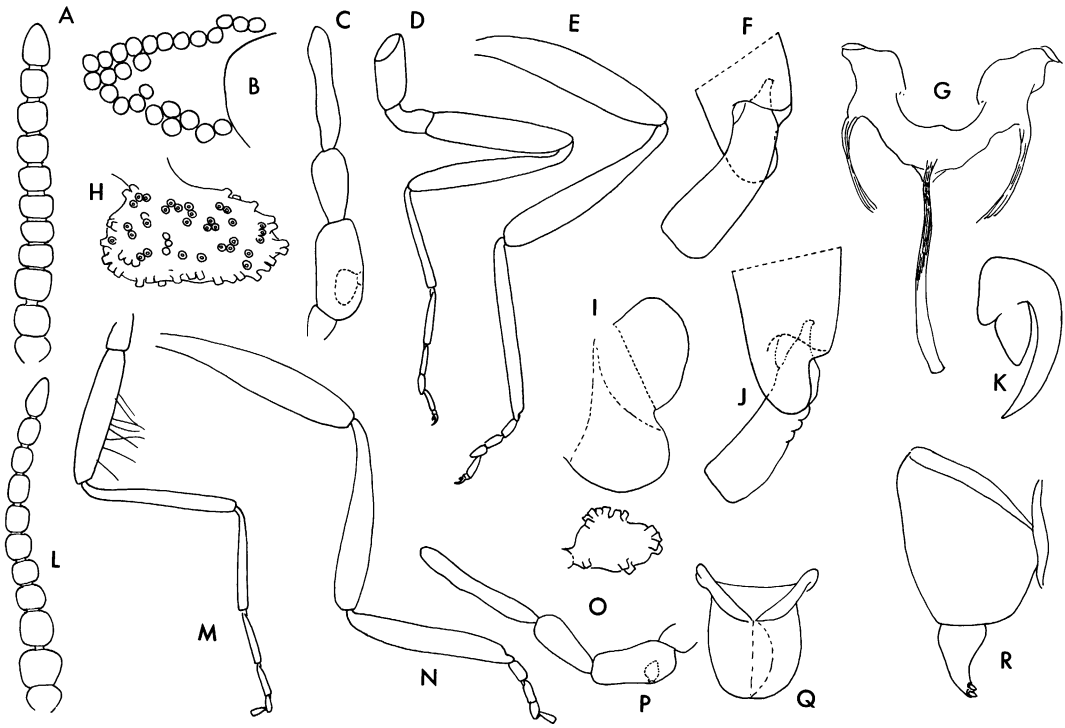

Fig. 47. *Gigantodax trifidus.* A–I. Female. **A.** Antenna. **B.** Fronto-ocular triangle. **C.** Maxillary palp. **D.** Foreleg. **E.** Hind leg. **F.** Calcipala, with second tarsal segment. **G.** Genital fork. **H.** Sensory vesicle of maxillary palp. **I.** Cercus and paraproct. **J.** Calcipala of male, with second tarsal segment. **K.** Claw of female. L–R. Male. **L.** Antenna. **M.** Foreleg. **N.** Hind leg. **O.** Sensory vesicle of maxillary palp. **P.** Maxillary palp. **Q.** Basal plate. **R.** Basimere and distimere.

es; only the median branch is bifurcate, very close to the base, giving in total four tertiary branches (fig. 48C). Filament gradually narrowed apicad, apex rounded. Microstructure of filaments as illustrated for *broyphyi.* Head and thorax of pupa light colored, covered by somewhat darker glabrous platelets. Distribution of platelets on clypeus as in figure 48B. Outline of female and male frontoclypeus as in figure 48E, M. Trichomes and platelets of thorax and frontoclypeus as in figure 48H. Onchotaxy of abdomen as in *antarcticus.*

Larva. Maximum length 7.5–8.0 mm. Width of head 0.80–0.85 mm. Body shape, color, cephalic apotome pattern, cervical sclerite, and histoblast of larva as in *antarcticus.* Antenna not reaching level of cephalic mouth fan stem. Antenna light brown; third segment almost as long as first and second combined (fig. 48I). Ratios of segments I–III = 1:0.8:1.5; terminal sensillum four times longer than width at base; cephalic fan with 25–26 rays. mandibular teeth as figure 48K, L, with 10–12 internal teeth and 11–12 mandibular serrations, the 2–3 basal ones being largest. Maxillary palp as shown in figure 48F. Hypostomium as in figure 48J. Hypostomial setae numbering from four to five, arranged in one irregular series. Anal sclerite as in *brophyi,* with scales and long setae. Crochet ring with 80–130 rows, each composed of 13–15 hooks. Recurrent struts well developed but some specimens not well pigmented distally.

HOLOTYPE: CHILE: *Santiago:* Quebrada del Rio Colorado, El Alfalfal, Los Maitenes, 1300 m, Oct. 10, 1972 (L. Pena and P. Wygodzinsky; AMNH), female.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, allotype male, five male paratypes and five female paratypes (all reared with associated pupal exuviae), pupae, and larvae. CHILE: *Santiago:* El Canelo, Ca-

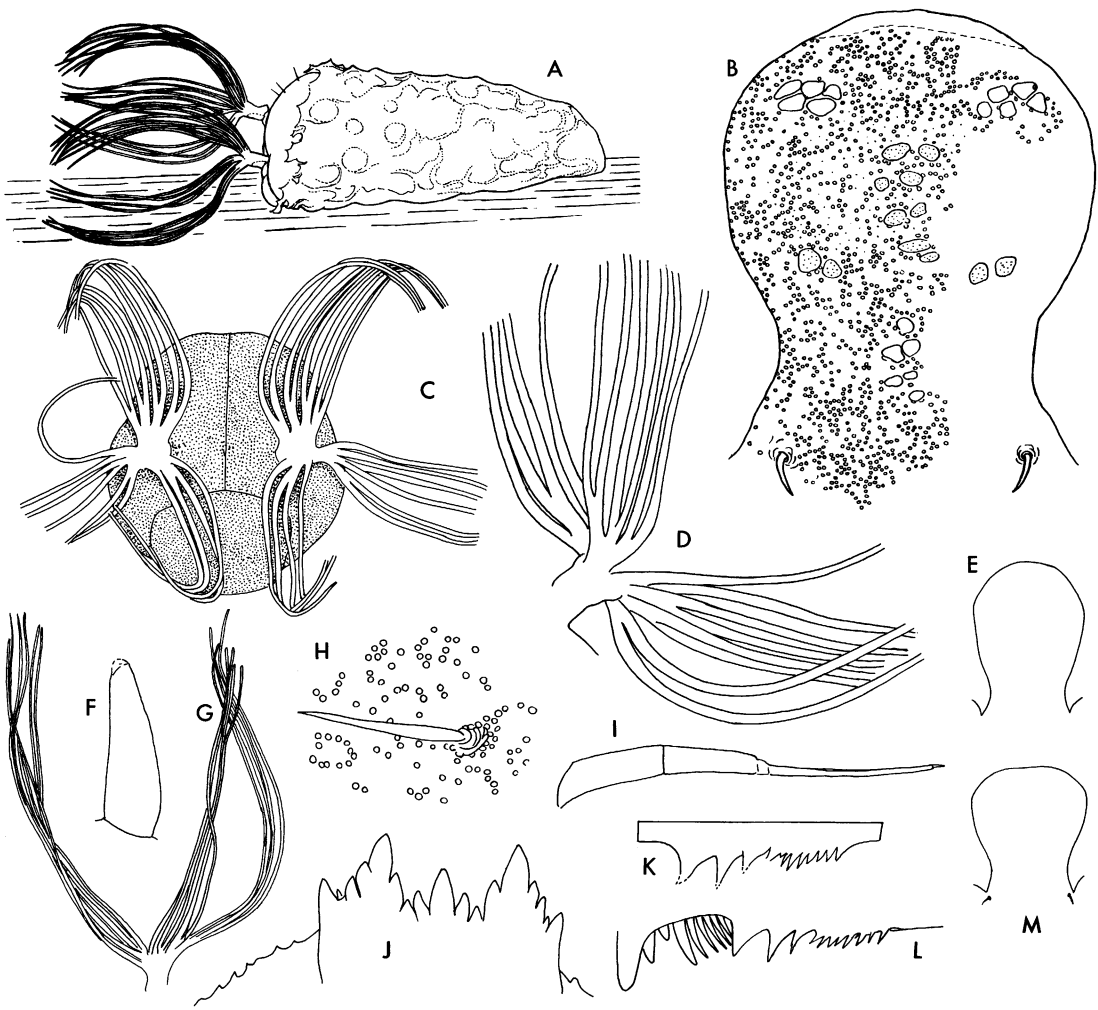

Fig. 48. *G. trifidus.* **A.** Pupa in cocoon, lateral view. **B.** Frontoclypeus of female. **C.** Anterior portion of body with gills, frontal view. **D.** Gill. **E.** Outline of frontoclypeus of male pupa. **F.** Maxillary palp of larva. **G.** Gill. **H.** Thorax of pupa, with trichome and platelets. **I.** Antenna of larva. **J.** Anterior portion of hypostomium. **K.** Mandibular serrations. **L.** Mandibular serrations, and apex of mandible. **M.** Outline of frontoclypeus of female.

jon of Rio Maipo, Nov. 1, 1967 (S. Coscarón; AMNH), 1 male paratype (reared, with associated pupal exuviae), 1 pharate female, pupae; ARGENTINA: *Neuquen:* Confluencia, Oct. 25, 1970 (S. Coscarón; AMNH), 1 male pharate (on slide); small creek on road 40, 30 km NE of Bariloche, Oct. 21, 1970 (S. Coscarón; MLP), 1 female with pupal exuviae, pupa (living with *antarcticum*). *Rio Negro:* Valle de los Vuriloches, Oct. 22, 1970 (S. Coscarón; MLP), pupae; Pampa Linda, 850 m, Oct. 22, 1970 (S. Coscarón; MLP), 1 female. *Mendoza:* Malargüe, Rio Salado, 15 km W highway 40, Sept. 21, 1975 (S. Coscarón; MLP), 1 male and 1 female (with pupal exuviae), pupae, and larvae.

ETYMOLOGY: The name refers to the three bundles of branches in pupal gill.

DISCUSSION: *Gigantodax trifidus* is very close to *G. antarcticus* and the following characters help to separate them (the characters of *antarcticus* given in parentheses): Antenna of female and male yellow brown (grayish brown); ratio of length/width of second palp

segment = 1:0.34–0.43 (=1:0.52–0.60); ratio length/width hind basitarsus of male = 1:5.5–5.9 (=1:4.2–5.0); female mandible with 28–36 teeth (27–30); pupal length 3.7–4.3 mm (4.7–5.5 mm); pupal gill branches arranged in three to four bundles (two bundles); platelets of frontoclypeus and pupal thorax sparse (dense); larval length 7.5–8.0 mm (9.0–9.7 mm); crochet ring of larva with 13–15 hooks per row (19–21). The pupa also could be confused with *G. rufidulus,* but that species has fewer platelets on the thorax and, with low magnification, it appears smooth; also the frontoclypeus platelets are more sparse and irregular in size.

Gigantodax femineus (Edwards)

Figures 49A–W, 50A–M

S. (Gigantodax) femineum Edwards, 1931: 135. Orfila, 1935: 1527.

Gigantodax femineum: Wygodzinsky, 1961a: 460, 1961b: 563. Vulcano, 1967: 3; 1977: 290. [Incorrect gender]

DIAGNOSIS: Recognized by the males with front and large fronto-ocular triangle, and pupal gills with the branches in a dorsal and ventral bundle, often joined apically making a ring in side view, more open than in *G. antarcticum,* but closer than in *G. fulvescens.*

REDESCRIPTION: *Female.* Length of wing 3.7–4.0 mm. Head black. Eyes black, antenna light brown, scapus and pedicellus yellow brown. Frons, clypeus, occiput, and maxillary palp brown; the first three with grayish polinosity. Thorax pale bronze yellow, setae of scutum, scutellum from yellow to golden, according to light. Wing transparent, space between Sc and R yellowish. Veins and setae of wing pale brown. Spines of wing dark brown. Legs very pale brown with the setae brass colored. Abdomen dark brown with posterior border of the tergites lighter colored. Legs of abdomen brass colored.

Frons as in figure 49V, with short median sulcus. Fronto-ocular triangle longer than wide (fig. 49B). Shape and proportions of the antennal articles as in figure 49J; maxillary palp as in figure 49A, with big sensory vesicle (fig. 49K). Maxilla with 28–31 teeth and mandible with 23–26 teeth. Hairs of antenna and scutellum as in *bryophyi.* Chaetotaxy of wing as in *antarcticus,* without spines on R_1. Shape, proportion, and arrangement of pigmentation of articles of fore and hind legs as in figure 49D, F. Calcipala longer than wide, extending almost to middle of length of tarsal segment II (fig. 49I). Claw as shown in figure 49H. Ratio length/width of hind basitarsus 7.1 (fig. 49L). Sternite VIII and gonapophyses as in figure 49O. Sternite VIII feebly sclerotized with about 25 setae on each side. Cercus and paraproct as in figure 49G. Border of cercus straight. Genital fork as in illustration 49E; spermatheca as in *antarcticus.*

Male. Length of wing 3.8 mm. Color as in female. Eyes dichoptic, with large facets only; interocular space as in figure 49W. Fronto-ocular triangle, small, approximately as high as wide (fig. 49C). Shape and proportions of antennal articles as in figure 49P. Maxillary palp as in figure 49Q, with sensory organ (fig. 49M) as in *antarcticus.* Maxilla with rugosities in the apex but not with teeth. Chaetotaxy of wing as in female. Shape and proportions of pigmentation of fore and hind legs as in figure 49R, S. Ratio length to width of posterior basitarsus = 5.1. Calcipala approximately as long as wide and shorter than half the length of posterior basitarsus (fig. 49T, U). Genitalia similar to those of *antarcticus.* Hooks of the endoparameres not observed. Basimere and distimere as shown in figure 49N.

Pupa. Cocoon of irregular shape, covering entire body to the base of the gills (fig. 50A). Fabric light brown, irregular, not very dense, frequently with adhering grains of sand or other particles of various sizes. Length of cocoon 4.5–5.0 mm. Length of body 4.0 mm. Length of gills in lateral view approximately 1.5 mm. Gills arranged in two groups, one dorsal and one ventral (fig. 50A, E–G), as in *antarcticus,* but without forming a large structure as in the former because the branches of *femineus* are very open, although more closed than in *fulvescens.* Head and thorax and abdomen light brown and covered with numerous platelets, especially on frons and genae. Frontoclypeus of female as in figure 50B and outline of male as in figure 50C; with abundant platelets (fig. 50B). Chaetotaxy of head, thorax, and abdomen as in *antarcticus.* Trichome and platelets of thorax as shown in figure 50K.

Larva. Maximum length 7.5–8.0 mm.

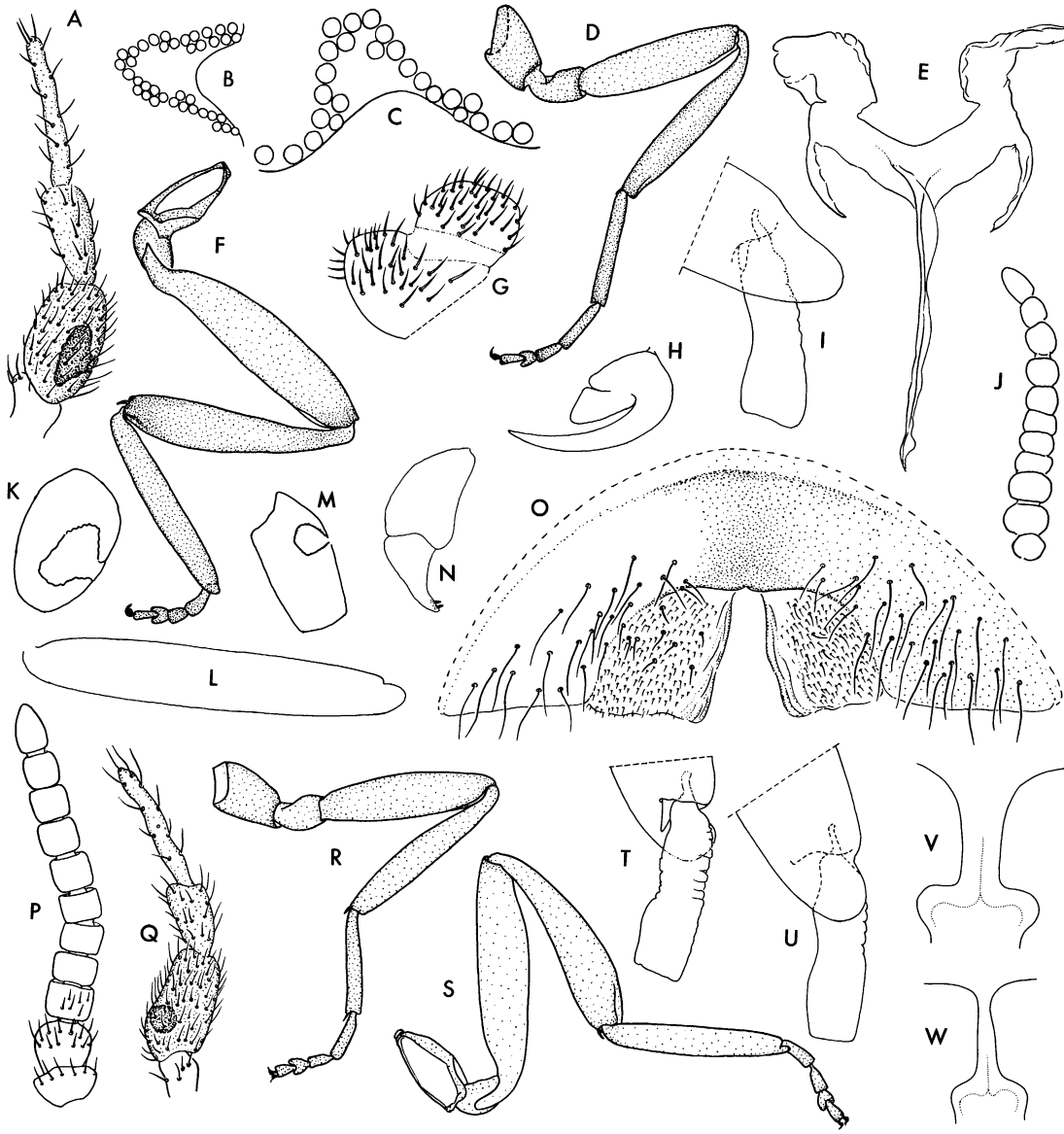

Fig. 49. *Gigantodax femineus.* A–O. Female. **A.** Maxillary palp. **B.** Fronto-ocular triangle. **C.** Same, different specimen. **D.** Foreleg. **E.** Genital fork. **F.** Hind leg. **G.** Cercus and paraproct. **H.** Claw. **I.** Calcipala, with second tarsal segment. **J.** Antenna. **K.** Second article of maxillary palp, wtih sensory vesicle. **L.** First hind tarsomere. **M.** Second article of maxillary palp of male. **N.** Basimere and distimere. **O.** Eighth sternite of female, with gonapophyses. P–U. Male. **P.** Antenna. **Q.** Maxillary palp. **R.** Foreleg. **S.** Hind leg. **T, U.** Calcipala, with second tarsomere. **V.** Frons, female. **W.** Same, male.

Maximum width of head 0.7–0.75 mm. Color light yellowish brown. Head clear chestnut brown. Cephalic apotome with ornamentation as shown in figure 50D, with the positive spots not very intense. Hypostomial bridge generally homogeneously pigmented, but some specimens show a lighter medium longitudinal hand. Antenna as in figure 50H. Ratio of segments I to III equal to 1:0.9:1.5. Cephalic fan with approximately 37 branch-

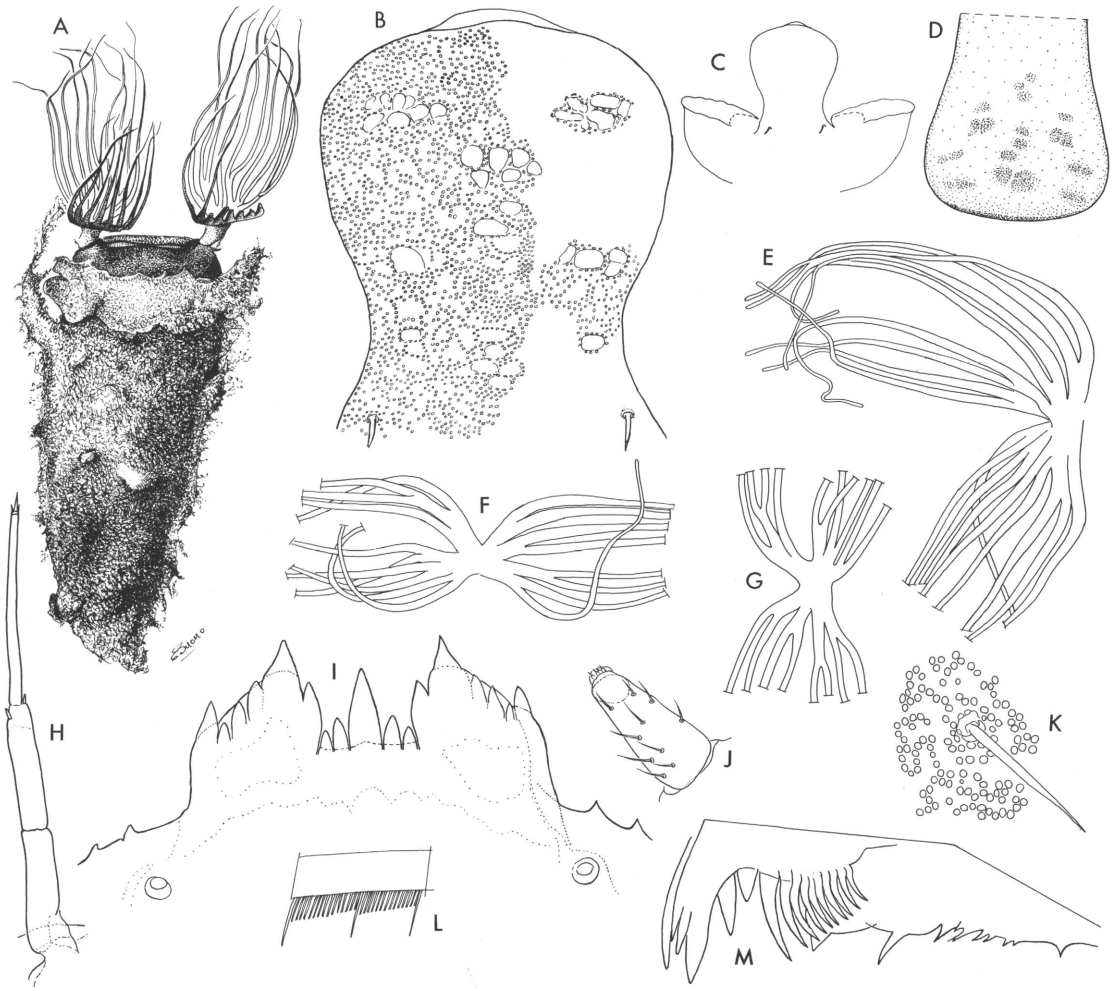

Fig. 50. *G. femineus.* A–G. Pupa. **A.** Pupa in cocoon, dorsal aspect. **B.** Frontoclypeus of female pupa showing disposition of platelets. **C.** Frontoclypeus of male pupa. **D.** Cephalic apotome of larva. **E–G.** Basal portions of gills of pupae. **H.** Antenna. **I.** Hypostomium. **J.** Maxillary palp of larva. **K.** Trichome of thorax of pupa. **L.** Detail of teeth of rays of cephalic fan of larvae. **M.** Apical portion of mandible of larva.

es; teeth brush as in figure 50L. Dentition of mandible as shown in figure 50M. Internal teeth numbering 8–9. Maxillary palp as in figure 50J. Hypostomium close to *brophyi.* Anterior portion well sclerotized as in figure 50I, with three to four bristles on each side. Gill histoblast similar to those of *antarcticus,* but with fewer fine filaments above. Aspect of anal disc as in *brophyi.* Number of series of hooks 95–103, with 16–19 hooks on each side.

MATERIAL EXAMINED: ARGENTINA: *Rio Negro:* Bariloche, November, 1926 (Shannon; USNM), 3 males, paratypes; Cerro Catedral, 1000 m, Nov. 25, 1950 (P. Wygodzinsky; AMNH), 5 reared females, 6 males, larvae and pupae; Pampa del Toro, 900 m, Nov. 29, 1950 (P. Wygodzinsky; AMNH), 7 females and 2 males, reared; Cerro Catedral, Arroyo la Cascada, larvae and 1 reared male; creek in Valle de los Vuriloches, Oct. 20, 1970 (S. Coscarón; MLP), 1 reared female, pupae and larvae.

BIOLOGY: Larvae and pupae were collected

on stones, in small creeks, with cool and crystalline waters.

DISCUSSION: Our material coincides well with the three paratype males belonging to the USNM. This species belongs to the complex of species with short calcipala, no spines on R_1 (*antarcticus, brophyi, rufidulus*) and *trifidus*. *Gigantodax femineus* can be distinguished by the coloration that in both sexes is yellowish, with yellow setae on the wing veins and legs. The male can also be recognized because it is dichoptic. The pupa can be differentiated easily from that of *rufidulus* because the latter has very scarce tubercles that appear smooth and shining at low magnification. All other species of the group possess abundant tubercles. *G. femineus* can be distinguished from *brophyi* because *brophyi* has the pupal gill base basketlike in shape, and the imagos are larger. It differs from *trifidus* in that the pupal gill branches in *femineus* are arranged in three bundles and the imagos are darker. It is also difficult to separate from *antarcticus,* but in that species, the imagos are generally darker and the branches of the pupal gill are in two bundles sometimes forming a circle; in some cases, the imagos of *antarcticus* are quite light colored and occasionally the filaments of the pupal gill are open wide (this is the case for specimens from Rio Turbio, Punta Arenas, and a few from Bariloche and Neuquen). *Gigantodax fulvescens* is smaller and the calcipala is almost as long as the second posterior tarsus. *Gigantodax marginalis* and *chilensis* are darker species, have a large calcipala, and have spines on R_1. *Gigantodax chilensis* has the wing membrane darker.

Gigantodax marginalis (Edwards)

Figures 51A–T, 52A–S, 53A–I, 54A–H

Simulium tarsatum Philippi, 1865: 634 (name preoccup. Macquart, 1863.

S. (*Gigantoxax*) *marginale* Edwards, 1931: 140. Orfila, 1935: 1529. Vargas, 1945: 158.

Gigantodax marginale: Wygodzinsky, 1961a: 460; 1961b: 563. Vulcano, 1967: 3; 1977: 290. [Incorrect gender]

Simulium philippianus Pinto, 1931 (new name *nec S. tarsatum* Philippi): 729. NEW SYNONYMY.

DIAGNOSIS: This species is characterized by the following combination of characters: calcipala length more than half of that of tarsomere 2, presence of spines on R_1, scutum light brown to dark brown; pupal gill branches thin basally and slowly curved at base; frontoclypeus and thorax with abundant smooth platelets; third antennal segment of larva distinctly longer than first.

Female. Length of wing 3.6–4.0 mm. Head dark. Eyes black, antenna, maxillary palp, clypeus, frons, and occiput grayish brown, scapus and pedicellus light brown, frons and clypeus with grayish pilosity; pilosity of frons very short, silvery, that of maxillary palp, frons, clypeus, and occiput longer and from silvery to light brown. Scutum, scutellum, metanotum, pleura, and legs from yellowish brown to dark reddish brown. Legs darker at the articulations and at the tarsi. Metanotum with grayish pollinosity. Hairs of scutum, scutellum, and legs from brass colored to yellowish brown. Legs somewhat darker. Wing translucent, veins yellowish brown, setae of the base of the wing from grayish to pale brown; setae of the veins pale yellowish brown. Halter pale brown. Abdomen from brownish gray to dark brown. Setae of first segment brass colored, very long, the remaining ones from the same color to dark brown and shorter.

Frons as in figure 51A. Fronto-ocular triangle somewhat wider than high (fig. 51B–D) Shape and proportions of antennal segments as shown in figure 51E. Maxillary palp as shown in figure 51F, G, showing a big variation in shape as shown in figure 51H–K of basal article, structure of sensory organ very much like that of *brophyi,* as are the mandible, maxilla, hypopharynx, and structure of the hair of the scutum and scutellum. Wing similar to those of *brophyi,* except the presence of spines on R_1, a small number of which appears beyond the termination of the costal cell. Spines arranged in a series of two rows alternating with hairs and smaller than those of the costa. Shape, proportion, and arrangement of pigment of the articulation of fore and hind legs as in figure 51L, M. Calcipala longer than wide, extending slightly beyond the middle of the second segment, three-fourths of the length (fig. 51N–P). Claw as shown in figure 51Q. Eighth sternite almost uniformly sclerotized and with approximately 30 setae of each side (fig. 51R). Cercus and

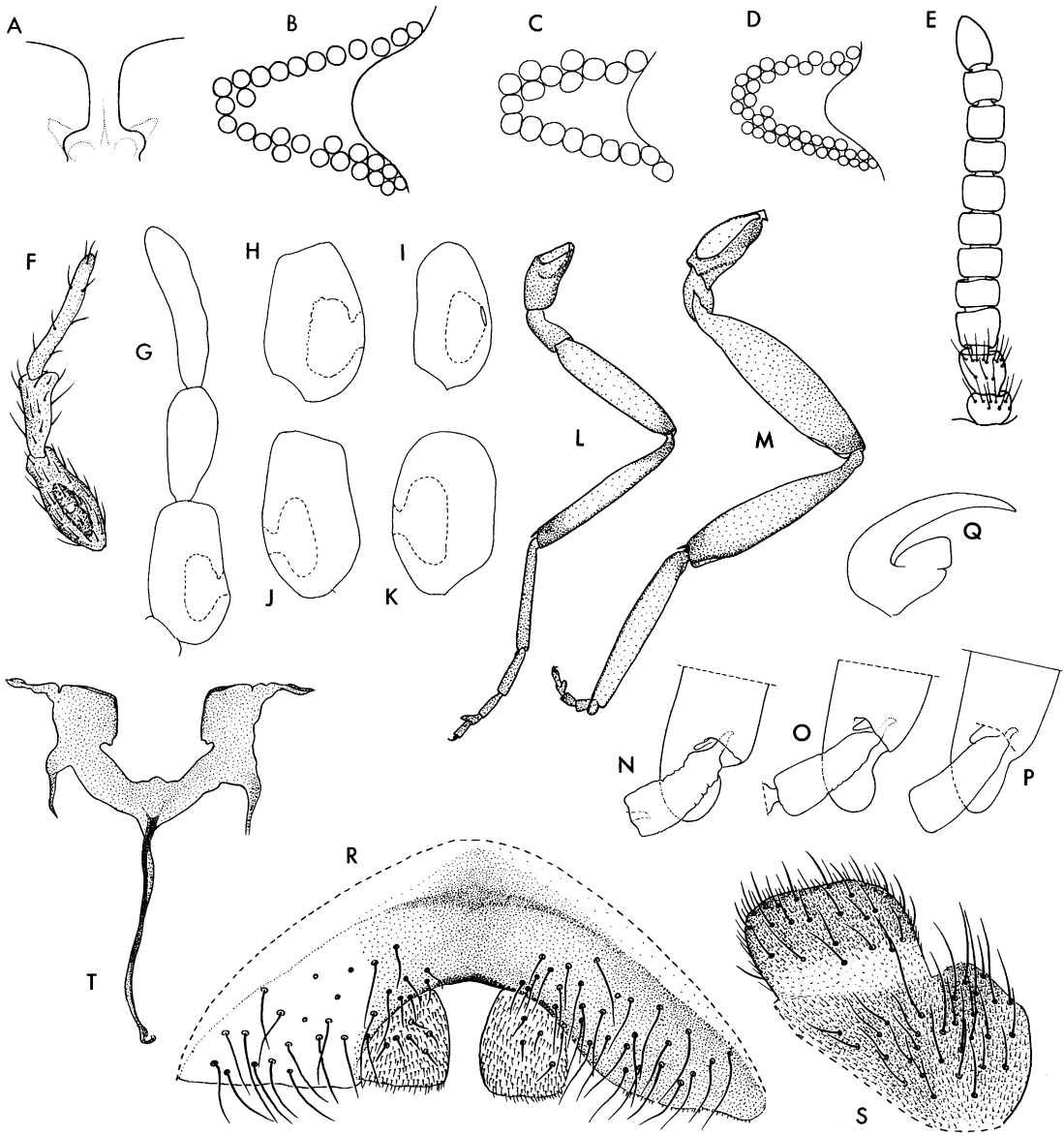

Fig. 51. *Gigantodax marginalis.* Female. **A.** Frons. **B–D.** Fronto-ocular triangle (B. Hua Hum, C. Peulla, D. Quebrada de La Plata). **E.** Antenna. **F, G.** Maxillary palp. **H–K.** Second segment of maxillary palp (H. Sierra de Nahuelbuta, I. Hua Hum, J. Quebrada de la Plata, K. Alto de Vilches). **L.** Foreleg. **M.** Hind leg. **N–P.** Calcipala, with second tarsal article (N. Quebrada de La Plata, O. Hua Hum, P. Peulla). **Q.** Claw. **R.** Eighth sternite, with gonapophyses. **S.** Cercus and paraproct. **T.** Genital fork.

paraproct as shown in figure 51S. Median branch of the genital fork delicate (fig. 51T).

Male. Length of wing 3.5–3.8 mm. Head blackish, eyes dark brown or violaceous; antenna, maxillary palp, clypeus dark grayish brown. Scapus and pedicellus dark reddish brown. Hairs of occiput, interocular space, clypeus, and palpi from light to dark brown. Thorax brown, scutum from dark grayish brown to black with the lateral borders yellowish brown; scutellum, metanotum, and pleura dark brown. Articulation of legs and

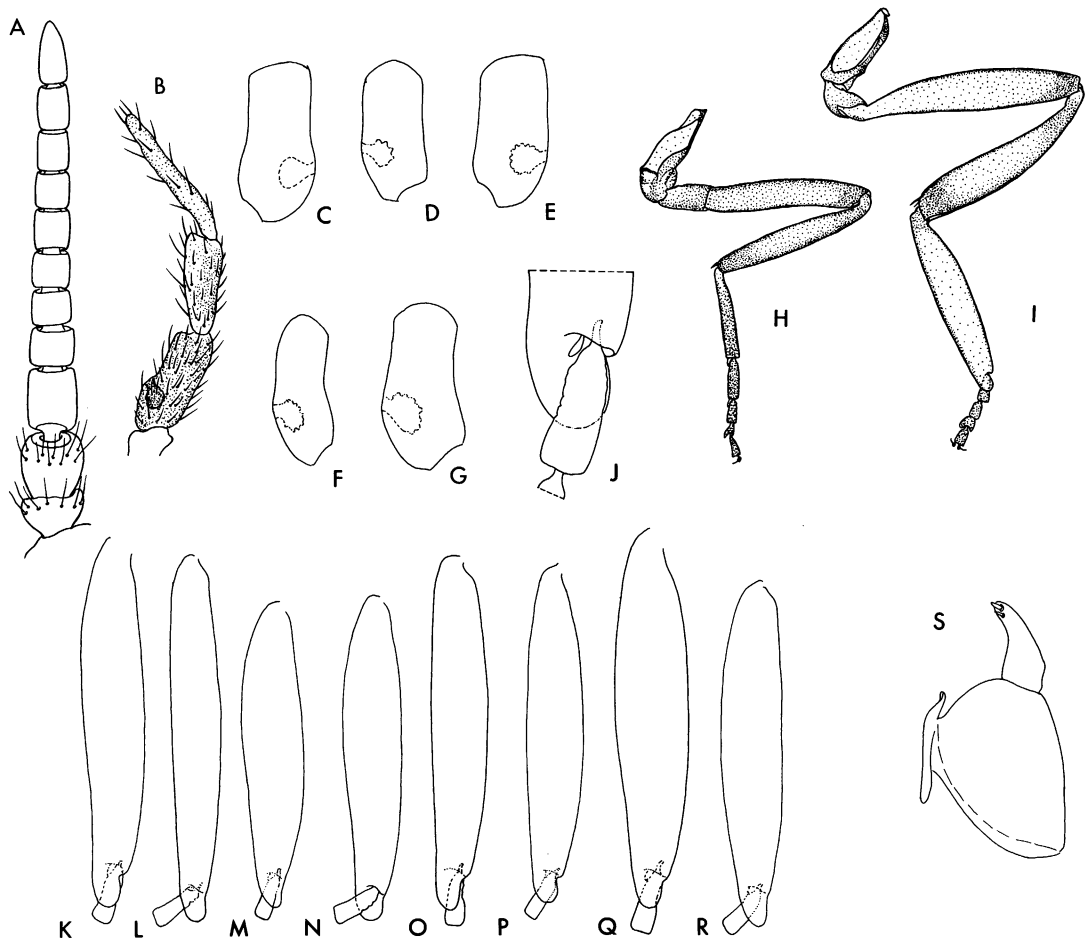

Fig. 52. *G. marginalis.* Male. **A.** Antenna. **B.** Maxillary palp. **C–G.** Basal segment of maxillary palp (C. Alto de Vilches, D. Hua Hum, E. Sierra de Nahuelbuta, F. Olmue, G. Rio Pico). **H.** Median leg. **I.** Hing leg. **J.** Calcipala. **K–R.** Posterior basitarsus, with second tarsal article (K. Hua Hum, L. Alto de Vilches, M. Olmue, N. Sierra de Nahuelbuta, O, Q, R. Lago Fontana, different specimens, P. Quebrada de La Plata). **S.** Basimere and distimere.

tarsi darkest. Hairs of scutum and scutellum from brass colored to dark brown. Setae of legs and wings brown. Abdomen dark brown dorsally, and grayish brown at sides. Setae of abdomen very long on first segment, remaining segments light brown or dark according to light. Antenna as in figure 52A. Maxillary palp as illustrated in figure 52B, but showing large variation on basal article (fig. 52C–G), with sensory organ similar to that of *antarcticus.* Shape, proportion, and distribution of pigmentation of the articles of the second and third legs as shown in figure 52H, I. Hind basitarsus with variable shape (fig. 52K–R). Ratio length to width of the posterior basitarsus 5.0:6.9. Calcipala longer than wide and extending beyond the middle of the length of the second posterior tarsal segment (fig. 52J). Wing as in female but in most cases spines of R_1 smaller and frequently confused with setae. Genitalia similar to those of *brophyi.* Distimere about half the length of basimere (fig. 52S).

Pupa. Cocoon brown with irregular, thick, fabric mesh. Cocoon covering the body to the base of the gills (fig. 53A). Length of cocoon

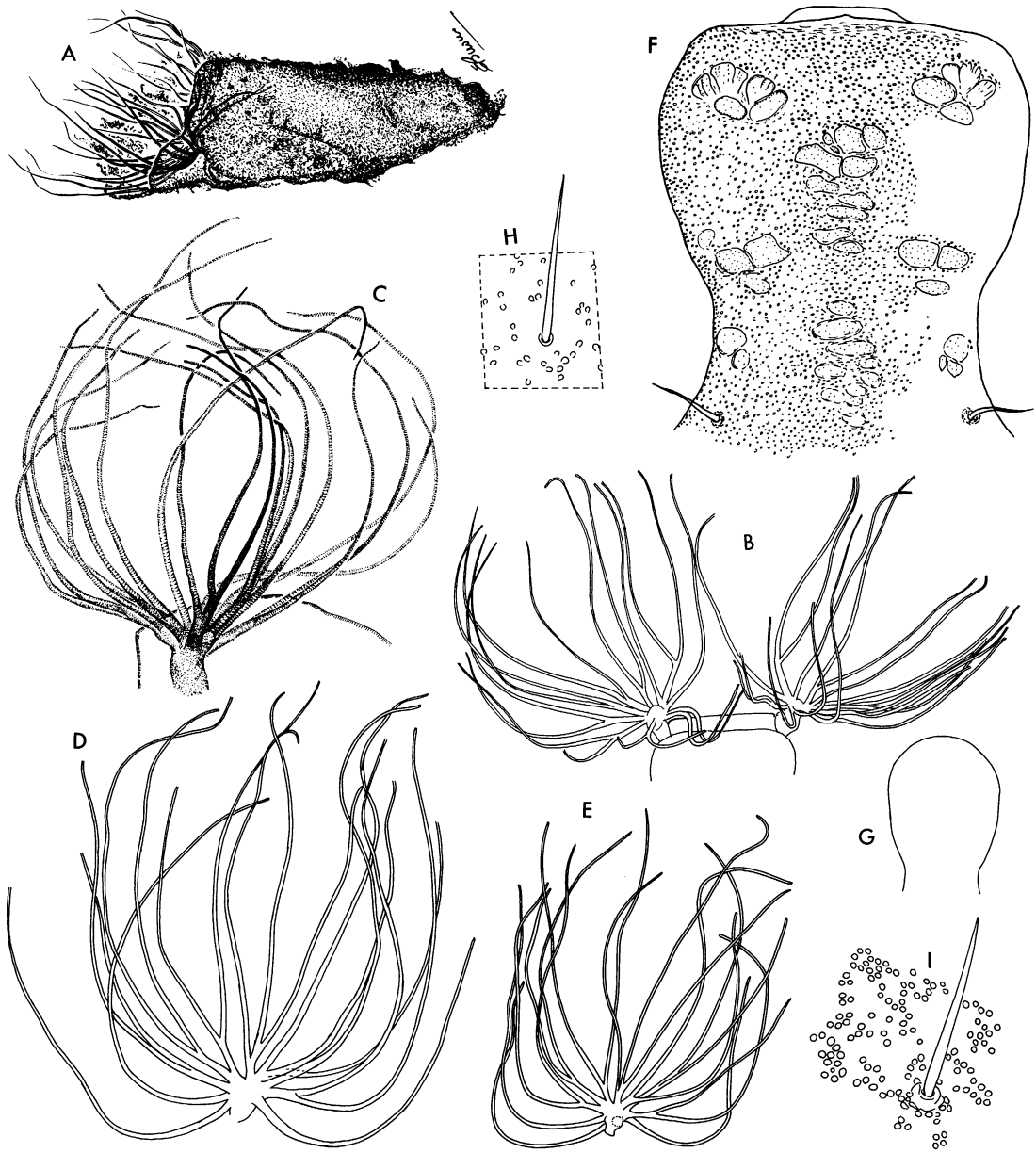

Fig. 53. *G. marginalis.* Pupa. **A.** In cocoon, lateral aspect. **B–E.** Gills. **F.** Frontoclypeus of female with platelets. **G.** Outline of frontoclypeus of male. **H, I.** Trichomes of thorax, with platelets.

4.5 mm in lateral view; length of the body of the pupa 3.8 mm. Cephalopterothecal length 2.5–2.7 mm. Length of gills in lateral view 1.5 mm. Gills arranged so as to form a "basket" when the branches of both sides are taken into account. The "basket" base is situated on the trunk, getting wider toward the middle with the branches converging apically (fig. 53A–E). Basal trunk short, giving rise to six primary branches; first branch subdividing at its base into three secondary branches, the median branch dividing again and forming three other tertiary branches. The first right primary branch is somewhat longer and gives

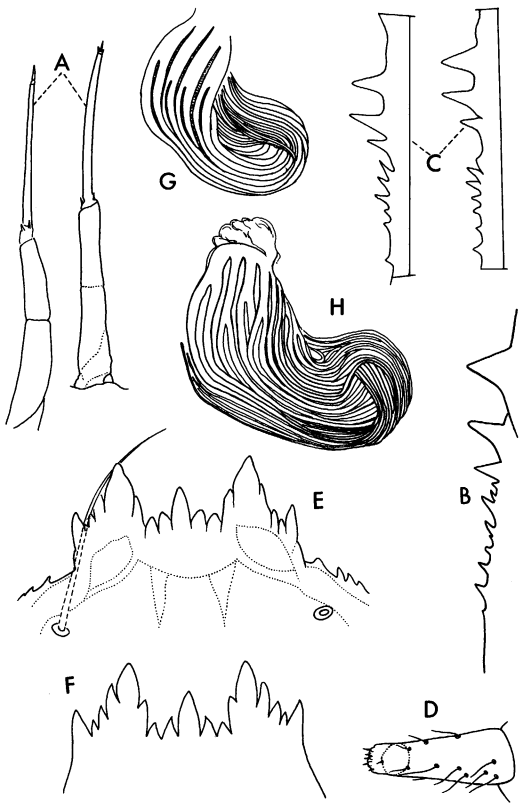

Fig. 54. *G. marginalis.* Larva. **A.** Antennae. **B, C.** Mandibular serrations. **D.** Maxillary palp. **E, F.** Teeth of hypostomium. **G, H.** Gill histoblast.

rise to three secondary branches. The left side once again subdivides to form two tertiary branches; the third primary branch is somewhat shorter than the anterior one and is subdivided into two branches with the right-hand one producing two tertiary branches. The fourth primary branch is very short and subdivided at its base into two branches, which immediately subdivide again, with each one forming two tertiary branches each. Fifth primary branch is longer, and subdivides into two branches. Sixth branch shorter, subdividing into two simple branches. Respiratory filaments pale grayish, variable according to locality examined. Filaments tapering gradually toward the apex. Microstructure as in *brophyi.*

Frontoclypeus and thorax light brown, covered with smooth platelets (fig. 53F), less numerous than in *antarcticus.* Frontoclypeus of female and male as shown in figure 53F, G. Distribution of platelets and chaetotaxy of thorax and abdomen as in *antarcticus.* Platelets and trichomes of thorax as shown in figure 53H, I.

Larva. Length 6.5–7.5 mm. Width of cephalic capsule 0.7 mm. Color pale grayish brown. Color of cephalic apotome very similar to that of *antarcticus.* Antenna shorter than stem of cephalic fan. Antenna as shown in figure 54A. Ratio of antennal segments I–III = 1:0.9:1.7. Terminal sensillum four times as long as wide at base. Cephalic fan with approximately 32 to 36 branches. Dentition of the mandible very similar to that of *antarcticus,* with seven to eight internal teeth. Variation of marginal teeth as in figure 54B, C. Maxillary palp as in figure 54D. General aspect of hypostomium as in *brophyi,* with three to five lateral setae. Margin of hypostomium as in figure 54E, F. Histoblast of pupal gill as shown in figure 54G, H. Structure of anal disc as in *brophyi* with 82–87 rows of hooks and 15–16 hooks in each row.

MATERIAL EXAMINED: ARGENTINA: *Chubut:* La Cancha, Lago Blanco, Feb. 8, 1969 ((S. Coscarón; MLP), 1 male, 1 female (with the pupal exuviae), pupae; Lago Fontana, Feb. 13, 1961 (S. Coscarón; MLP), 5 females, 5 males (with pupal exuviae), pupae; Arroyo Blanco, Lago Fontana, Feb. 14, 1961 (S. Coscarón; MLP), 1 female (with pupal exuviae), pupae; Lago Vintter, Feb. 18, 1961 (S. Coscarón; MLP), 1 female (with pupae exuviae), pupae; Alto Rio Mayo, Feb. 16, 1961 (S. Coscarón; MLP), pupae; Rio Pico, Feb. 18, 1961 (S. Coscarón; MLP), 1 male pharate, 1 male (with pupal exuviae), pupae; Lago Puelo, Nov. 28, 1950 (P. Wygodzinsky; AMNH), 2 males, 3 females (with pupal exuviae); Lago Futalaufquen, Feb. 2, 1975 (S. Coscarón; MLP), 1 male (with pupal exuviae), pupae. *Rio Negro:* Bariloche (Shannon; USNM); paratypes; Nov. 1926, 1 female; Nov. 5–10, 1926, 1 male; Dec. 1, 1926, 2 males; Bariloche, Nov. 27, 1950 (P. Wygodzinsky; AMNH), 1 male, 4 females (with pupal exuviae), pupae; Bariloche, 4 km E of Llao-Llao, 760 m (Schlinger; Riverside), 1 male; Bariloche, Rio Nirihuau, Oct. 24, 1970 (S. Coscarón; MLP), pupa; Bariloche, small creek near Rio Manso, Oct. 22, 1970 (S. Coscarón; MLP), 4 males and 2 females (with pupal exuviae), pupae; Bariloche, Rio Limay, Nov. 23, 1950 (P. Wy-

godzinsky; AMNH), pupa; Bariloche, small creek near Bahia Lopez, Jan. 22, 1971 (S. Coscarón; MLP), 1 male, 1 female (with pupal exuviae), pupae and larvae; Bariloche, Arroyo La Virgen, Jan. 22, 1971 (S. Coscarón; MLP), pupa; Bariloche, Colonia Suiza, (S. Coscarón; MLP), Sept. 27, 1975, Jan. 17, 1983, pupae and larvae, pupae; Bariloche, Rio Guillermo, Jan. 23, 1971 (S. Coscarón; MLP), pupae; Lago Frias, Feb. 18, 1967 (S. Coscarón; AMNH), 2 males; pupae; Bariloche, Lago Moreno (P. Wygodzinsky; AMNH), Nov. 24, 1950, 2 males (with pupal exuviae); Bariloche, Lago Trebol, Nov. 25, 1950 (P. Wygodzinsky; AMNH), 1 female (with pupal exuviae); Lago Mascardi, Feb. 15, 1967, Feb. 3, 1984 (S. Coscarón; AMNH), larvae, pupa, females, and males. Base of Cerro Lopez, Feb. 9, 1977 (S. Coscarón; MLP), pupae; Arroyo Lopez, Feb. 3, 1984 (S. Coscarón; MLP), larvae and pupae. Arroyo on Circuito Chico, Feb. 2, 1984 (S. Coscarón; MLP), pupae and larvae. *Neuquen:* Arroyo Chacabuco, 5 km N of Lake Nahuel Huapi, Feb. 15, 1967 (S. Coscarón; AMNH), pupae; same, Oct. 23, 1970 (S. Coscarón; MLP), pupae; Feb. 3, 1984, pupae and larvae. Arroyo Llao-Llao, Jan. 9, 1968 (S. Coscarón; MLP), pupae; Arroyo Puipocon, Jan. 10, 1968 (S. Coscarón; MLP), pupa; 30 km NE of Bariloche, Oct. 22, 1970 (S. Coscarón; MLP), pupae; Valle Encantado, Oct. 21, 1970 (S. Coscarón; MLP), pupae; La Lipela, Jan. 24, 1971 (S. Coscarón; MLP), pupae; road to La Angostura, 20 km W of highway 40, Jan. 29, 1971 (S. Coscarón; MLP), pupae; same, Sept. 25, 1975, 1 female (with pupal exuviae); N of Nahuel Huapi, arroyo on highway, Sept. 25, 1975 (S. Coscarón; MLP), 1 female (with pupal exuviae); Confluencia, Oct. 25, 1970 (S. Coscarón; MLP), pupae; Hua-Hum, Parque Lanin, Jan. 16, 1968 (S. Coscarón; MLP), 4 males, 4 females (with pupal exuviae), pupae; Pucara, Parque Lanin, Feb. 20, 1967 (S. Coscarón; AMNH), pupae; San Martin de los Andes, Jan. 6, 1962 (S. Coscarón; MLP), 1 male (with pupal exuvium; San Martin de los Andes, Jan. 1941 (Bridaroli), 2 females; Arroyo Yuco, Jan. 29, 1979 (S. Coscarón; MLP), pupae, same, Apr. 1, 1979, Jan. 8, Apr. 30, 1980, Apr. 3, May 3, June 4, Nov. 2, 1982, Feb. 7, 1983 (Gentili; MLP), larvae, pupae, and females; Arroyo Quiltrahue, Jan. 28, Feb. 20, 1979; Jan. 25, Feb. 1, 1980, Feb. 19, Nov. 10, 1981 (Gentili; MLP) pupae, females, and males; arroyo Chidiak Jan. 8, 1980 (Gentili; MLP), larvae; arroyo Trompul, Oct. 3–4, 1981 (Gentili; MLP), 2 females; arroyo de la Telesilla, Mar. 3, Apr. 1, May 3, June 6, July 7, Aug. 2, Sept. 10, Oct. 2, Nov. 3, 1982, Jan. 3, Feb. 7, Mar. 29, July 1, 1983 (Gentili; MLP), larvae, pupae; Arroyo Culebra, Apr. 1, May 2, 1982, Mar. 29, 1983 (Gentili; MLP), larvae; arroyo Quilaniahue, Jan. 22, 1979 (S. Coscarón; MLP), 1 pupa, Mar. 28, 1982 (Gentili; MLP), larvae; Creek on lake Lacar, Jan. 3, 1978 (S. Coscarón; MLP), pupae and larvae; S.M. de los Andes, Feb. 8, 1967 (S. Coscarón; AMNH), 1 female (with pupal exuviae), pupae. CHILE: *Llanquihue:* El Frutillar, Sept. 20, 1954 (Kuschel; MHN), 1 female; 20 km W of Ensenada, Feb. 8, 1967 (S. Coscarón, AMNH), pupae; arroyo near Ensenada, Feb. 9, 1967 (S. Coscarón, AMNH), pupae; 8 mi W of Puerto Varas, Jan. 16, 1951 (Ross and Michelbacher; CAS), 3 females; Peulla, Feb. 10, 1967 (S. Coscarón; AMNH), 2 females, 2 males (with pupal exuviae) and pupae. *Osorno:* Villarrica, Nov. 26, 1963 (F. Edmunds; CAS), pupa. *Valdivia:* Corral, Feb. 3, 1967 (S. Coscarón; AMNH), 1 pupa; Rio Llollehue, puente Itropulli, W of Ranco, Feb. 4, 1967 (S. Coscarón; AMNH), pupa. *Cautin:* 12.3 km N of Loncoche, 280 m, Nov. 10, 1966 (E. Schlinger-Irwin; CIS), 1 female; 20 km NE of Loncoche, Feb. 2, 1967 (S. Coscarón; AMNH), 1 female (with pupal exuviae), pupae; 9 km E of Loncoche, Feb. 2, 1967 (S. Coscarón; AMNH), 1 female (with pupae exuviae), pupae; 25 km E of Temuco, June-July, 1961 (M. G. Smith; CAS), 1 male. *Malleco:* Rio Blanco, 1100–2000 m, Feb., 1964, (L. Pena; CAS), 4 females and 5 males; Pehuenco, Jan. 13–17, 1963 (L. Pena; CIS), 2 females; Cordillera de Nahuelbuta, W of Angol, 1220 m, Feb. 12, 1967 (E. Schlinger; CIS), 1 female; Sierra de Nahuelbuta, W of Angol, 1200 m, Jan. 3, 1951 (Ross and Michelbacher; CAS), 4 females, 4 males; Angol, Oct. 18, 1931 (Bullock; USNM), 2 males, 3 females; 22 km E of Temuco, June–July 1951 (M. G. Smith; CAS), 1 female; Gualletue, 1200 m, Dec. 14, 1963, 1 female; Tolguaca, Jan. 9, 1962 (R. Usinger; CAS), 4 females. *Bio-Bio:* El Abanico, Dec. 31, 1950 (Ross and Michelbacher;

CAS), 1 female. *Concepcion:* Rinconada de Curcura, 3 km S of Lota, Oct. 12, 1972 (S. Coscarón; MLP), pupae; Escuadron, SE of Concepcion, Oct. 72 (S. Coscarón; MLP), 1 male, 1 female with pupal exuviae (Ross and Michelbacher; CAS), 4 males, 4 females. *Nuble:* Las Cabras, Vulcan Chillan, 1200–1400 m, Dec. 20–23, 1954 (L. Pena; CNC), 1 female; Chillan, near Agricultural Experimental Station, Oct. 10, 1972 (S. Coscarón; MLP), 7 males, 4 females (with the pupal exuviae), pupae. *Talca:* Alto de Vilches, Oct. 30, 1969 (J. Rozen, L. Pena; AMNH), 40 females, 10 males; Alto de Vilches, Oct. 5, 1972 (S. Coscarón, L. Pena, and P. Wygodzinsky; AMNH), 1 female. *Curico:* El Coigual, Jan. 20–26, 1964 (L. Pena; CAS), 1 male; Cajon del Rio Claro SE of Los Quenes, 1000–1200 m, Oct. 9, 1966 (E. Schlinger; CIS), 3 females. *Santiago:* Capital, May 15, 1951 (Kuschel; MHN), 1 female; El Manzano, June 4, 1951 (Kuschel; MHN), 1 female; El Canelo, 880 m, Dec. 4, 1963 (F. Edmunds; CNC), 1 male; Marga Marga, Nov. 11, 1927 (USNM), 11 females, 1 male; Cuesta El Chada, 550 m, Oct. 12, 1972 (L. Pena and P. Wygodzinsky; AMNH), 3 females, 2 males (with the pupal exuviae), pupae; Rungue, El Roble Road, Oct. 11, 1972 (L. Pena and P. Wygodzinsky; AMNH), 3 females, 3 males (with pupal exuviae), pupae; 4 km SW of El Caleu, Oct. 11, 1972 (L. Pena and P. Wygodzinsky; AMNH), 2 males, 3 females (with pupal exuviae), pupae; Maipu, Quebrada de la Plata, 1966, malaise trap (M. I. Irwin; CIS), April 26, 1 female; June 1, 1 male, 1 female; June 24, 2 females, 1 male; July 30, 4 females, 1 male; Aug. 3, 2 females; Aug. 4, 2 females; Aug. 5, 1 female; Aug. 7, 3 females; Aug. 8, 3 females; Aug. 10, 1 female; Aug. 15, 5 females; Aug 16, 2 females; Aug. 18, 12 females; Aug. 22, 3 females; Aug. 24, 10 females; Aug. 29, 2 females; Aug. 31, 1 female; Sept. 10, 13 females, 1 male; Sept. 19, 4 females; Sept. 29, 1 female; Sept. 30, 2 females; Oct. 6, 1 female; Oct. 9, 2 females Quebrada de la Plata, Oct. 16, 1967 (S. Coscarón; AMNH), 9 females, 9 males (with pupal exuviae), pupae and larvae; Quebrada de la Plata, Oct. 12, 1972 (L. Pena and P. Wygodzinsky), 1 female (with the pupal exuviae). *Valparaiso:* Olmue, Oct. 9, 1967 AMNH) 1 male (with pupal exuviae) and pupae; Olmue, foot of Cerro Campana, Oct. 19, 1967 (S. Coscarón; AMNH), 1 female (with pupal exuviae).

BIOLOGY: This species breeds in small creeks on leaves, stones, and other substrates. It is very abundant in the northern Patagonian Andes, especially in the summer, frequently in waters of relatively high temperature.

DISCUSSION: *Gigantodax marginalis* shows substantial variation in body coloration especially of the male (which is generally darker), the shape of the hind basitarsus, and the basal segment of the palpus. The closest species, *luispenai* and *kuscheli,* are difficult to separate from *marginalis. Gigantodax luispenai* has more homogeneous gray-brown pigmentation (without light borders), the setae on the scutum are more sparse, the males with the hind basitarsus thinner (ratio length/width 6.0–6.5), and the pupae are darker and have more erect gill branches. *Gigantodax kuscheli* has the thorax light reddish brown, the metanotum piceous, and lacks spines on R_1.

Gigantodax kuscheli Wygodzinsky

Figures 55A–P, 56A–O

Gigantodax kuscheli Wygodzinsky, 1952: 81–85, ill. Coscarón and Wygodzinsky, 1962: 308–310, ill. Vulcano, 1967: 3; 1977: 290.

DIAGNOSIS: Very generalized species with same coloration as light specimens of *G. marginalis*; larvae very close to *fulvescens*; pupae unknown.

REDESCRIPTION: *Female.* Maximum wing length 4 mm. Frons and clypeus blackish, antenna piceous with basal articles dark orange. Scutum, scutellum, and pleurae pale yellowish brown; metanotum piceous; wing veins and legs light brown. Abdomen dark brown.

Fronto-ocular triangle wider than high (fig. 55A). Antenna as in figure 55B. Ratio length/width of second article of maxillary palp = 1:0.54, with sensory vesicle more than half the length of article (fig. 55C). Wing with spinules on R_1 as figure 55D. Foreleg as in figure 55E. Ratio length/width of hind basitarsus = 6.8. Calcipala about three-fourths length of tarsomere 2 (fig. 55F, G). Claw shape as shown in figure 55H. Genitalia close to *marginalis*; genital fork as in figure 55I.

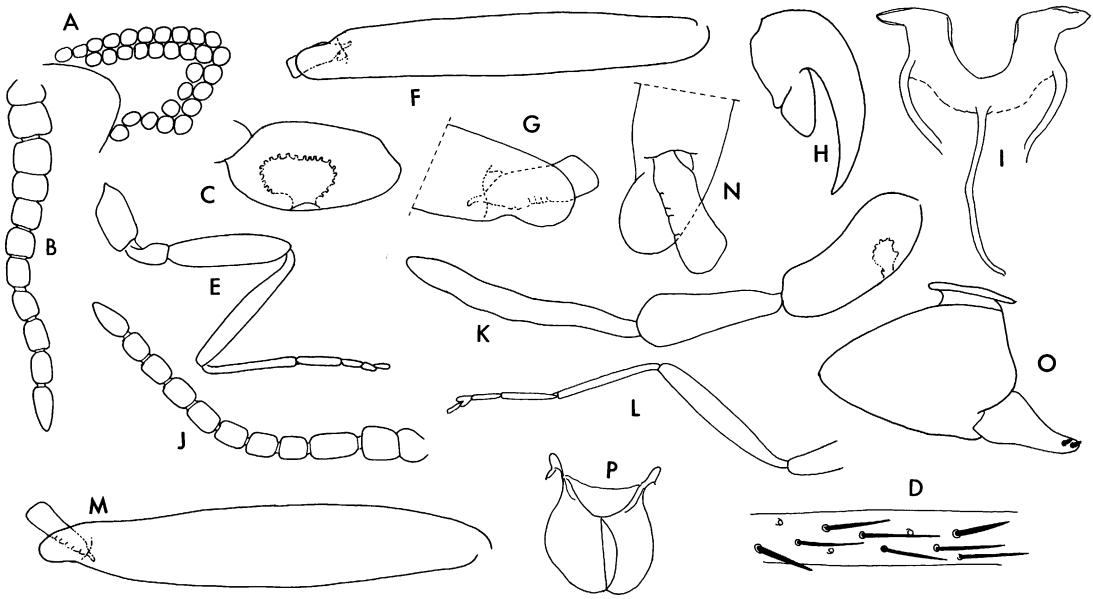

Fig. 55. *Gigantodax kuscheli.* A–I. Female. **A.** Fronto-ocular triangle. **B.** Antenna. **C.** Second article of maxillary palp, with sensory vesicle. **D.** Setae and spiniform setae on R_1. **E.** Foreleg. **F.** Posterior basitarsus, with second tarsal segment. **G.** Calcipala, with second tarsal segment. **H.** Claw. **I.** Genital fork. J–P. Male. **J.** Antenna. **K.** Maxillary palp. **L.** Foreleg. **M.** First tarsomere of hind leg. **N.** Calcipala. **O.** Basimere and distimere. **P.** Ventral plate.

Male. Wing length 3.3–4.0 mm. Coloration as in female, but scutum dark orange, sometimes with central area dark brown. Antenna as in figure 55J; maxillary palp with basal article nearly three times as long as wide (fig. 55K). Sensorial vesicle about half as wide as basal article. Articles of foreleg as in figure 55L. Ratio length/width of hind basitarsus = 5.6 (fig. 55M). Calcipala about as long as wide and approximately three-fourths the length of tarsomere 2 (fig. 55N). Distimere about half the length of basimere (fig. 55O), with two apical hooks; ventral plate as in figure 55P.

Pupa. Unknown.

Larva. Maximum length 8.0 mm; maximum width of cephalic capsule 0.73 mm. Shape as in figure 56A. Head light brown, cephalic apotome as in figure 56B. Cephalic capsule ventrally as in figure 56C. Antenna as long as or shorter than stem of cephalic fan. Antenna as shown in figure 56D; ratio of articles I–III = 1:0.8:1.4–1.5. Terminal sensillum 3–4 times as long as wide at base. Cephalic fan with about 31 rays; disposition of ray teeth as in figure 56E. Mandible with 9–10 internal teeth and 7–9 marginal serrations (fig. 56F, G). Maxillary palp (fig. 56H) with ratio length/width = 2. Hypostomium with 4–5 lateral trichomes. Median tooth at same or below level of corner teeth (fig. 56I–K). Proleg sclerite with about 33 teeth (fig. 56L). Anal sclerite as in figure 56M, with abundant scales. Crochet ring with 106–107 rows of 20–23 hooks each. Recurrent struts well pigmented. Gill histoblast as in figure 56N, O.

DISTRIBUTION: CHILE: Islas de Juan Fernandez.

BIOLOGY: Unknown.

DISCUSSION: The known adult specimens are very close to light-colored specimens of *marginalis.* The larva has a hypostomium close to *chilensis* and *dryadicaudicis.* It will be necessary to find the pupa in order to clarify our knowledge of this species.

Gigantodax luispenai, new species
Figures 57A–R, 58A–K

DIAGNOSIS: Relatively small species, adults gray-brown with few spines on R_1, pupa with

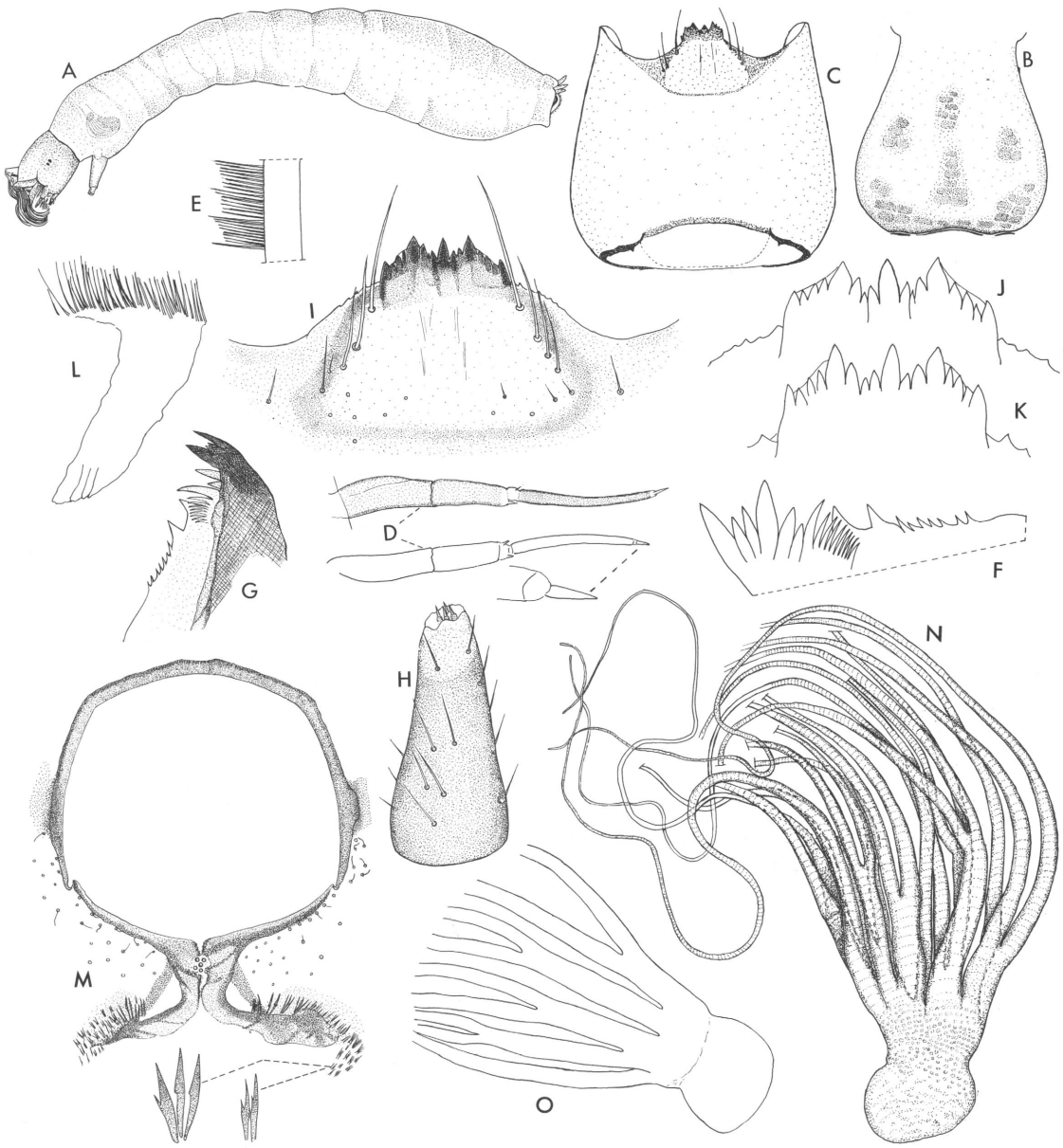

Fig. 56. *G. kuscheli.* A–M. Larva. **A.** Larva, lateral view. **B.** Cephalic apotome. **C.** Cephalic capsule, under surface. **D.** Antennae. **E.** Teeth of rays of mouthfans. **F.** Apex of mandible. **G.** Apex of mandible. **H.** Maxillary palp. **I.** Hypostomium. **J, K.** Anterior portion of hypostomium. **L.** Lateral sclerite of proleg. **M.** Anal sclerite. **N.** Gill histoblast, somewhat opened. **O.** Base of histoblast.

abundant platelets on frontoclypeus and thorax.

DESCRIPTION: *Female.* Length of wing 3.3–3.6 mm. Head dark. Eye black. Antenna, maxillary palp, clypeus, frons, and occiput grayish brown. Scapus and pedicellus light brown. Frons and clypeus with gray pollinosity. Setae of antenna silvery, very short, those of the maxillary palp, frons, clypeus, and occiput longer and their color from light

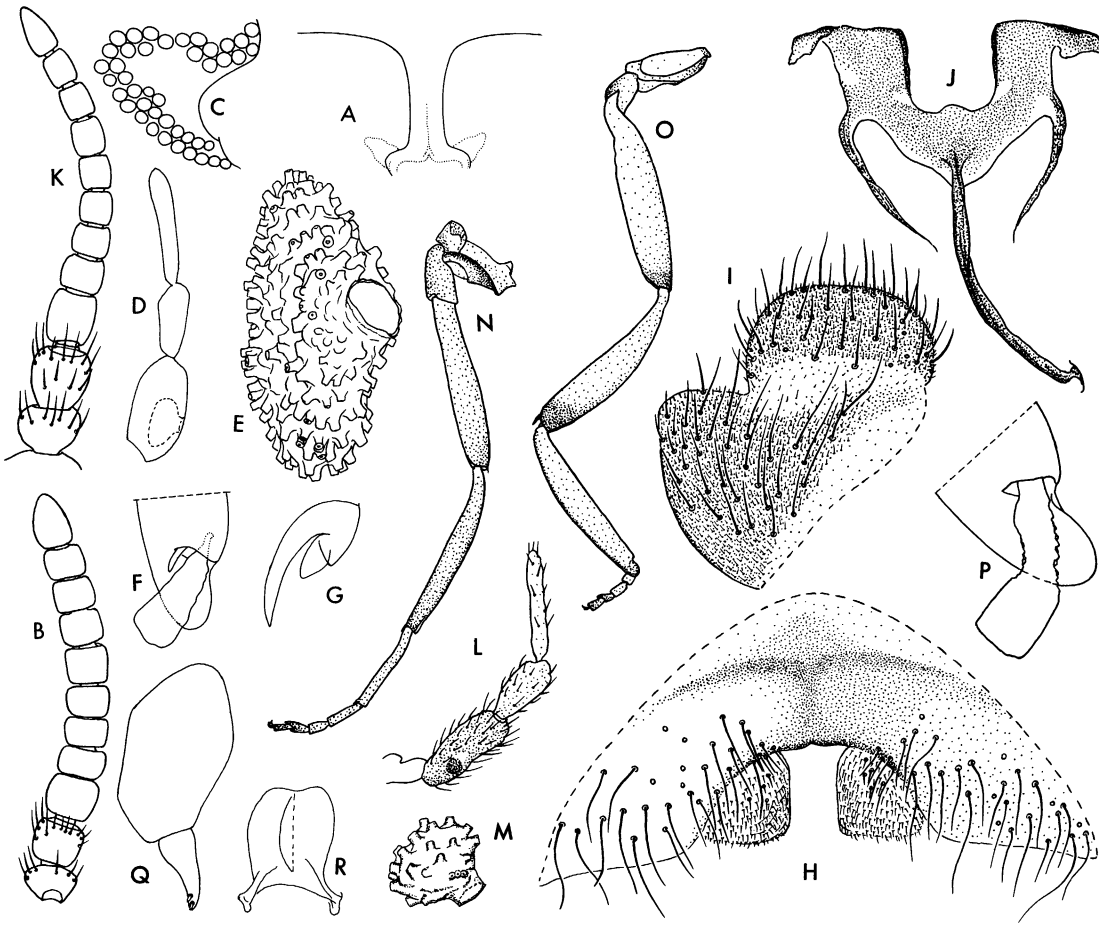

Fig. 57. *Gigantodax luispenai.* A–J. Female. **A.** Frons. **B.** Antenna. **C.** Fronto-ocular triangle. **D.** Maxillary palp. **E.** Sensory vesicle. **F.** Calcipala, with second tarsal segment. **G.** Claw. **H.** Eighth sternite, with gonapophyses. **I.** Cercus and paraproct. **J.** Genital fork. K–R. Male. **K.** Antenna. **L.** Maxillary palp. **M.** Sensory vesicle. **N.** Median leg. **O.** Hind leg. **P.** Calcipala, with second tarsal segment. **Q.** Basimere and distimere. **R.** Ventral plate.

brown to silvery. Scutum, scutellum, pleura, and metanotum dark reddish castaneous; pleura and metanotum with grayish pollinosity. Setae of scutum and scutellum silvery brass. Wing transparent, veins brown with hairs grayish to pale brown. Legs grayish brown, darker at articulations and on the tarsi. Hairs of legs from grayish brown to dark brown (according to light). Frons with small median sulcus (fig. 57A). Fronto-ocular triangle longer than wide (fig. 57C). Shape and proportion of antennal segments as shown in figure 57B. Mandible with 24 teeth. Ratio length/width of second segment of maxillary palp = 1:0.61 (fig. 57D). Sensory vesicle of maxillary palp as in figure 57E. Maxilla with approximately 35 teeth. Setae of scutum and scutellum as in *brophyi.* Wing as in *marginalis* and generally with fewer spines than in R_1. Calcipala longer than wide, extending beyond the middle of the length of the basitarsus (fig. 57F). Basal tooth of claws as shown in figure 57G. Genitalia very similar to those of *marginalis.* Sternite VIII and gonapophyses as in figure 57H. Sternite with approximately 35 setae on each edge. Cercus, paraproct, and genital fork as shown in figure 57I, J.

Male. Wing length 3.4 mm. Head blackish,

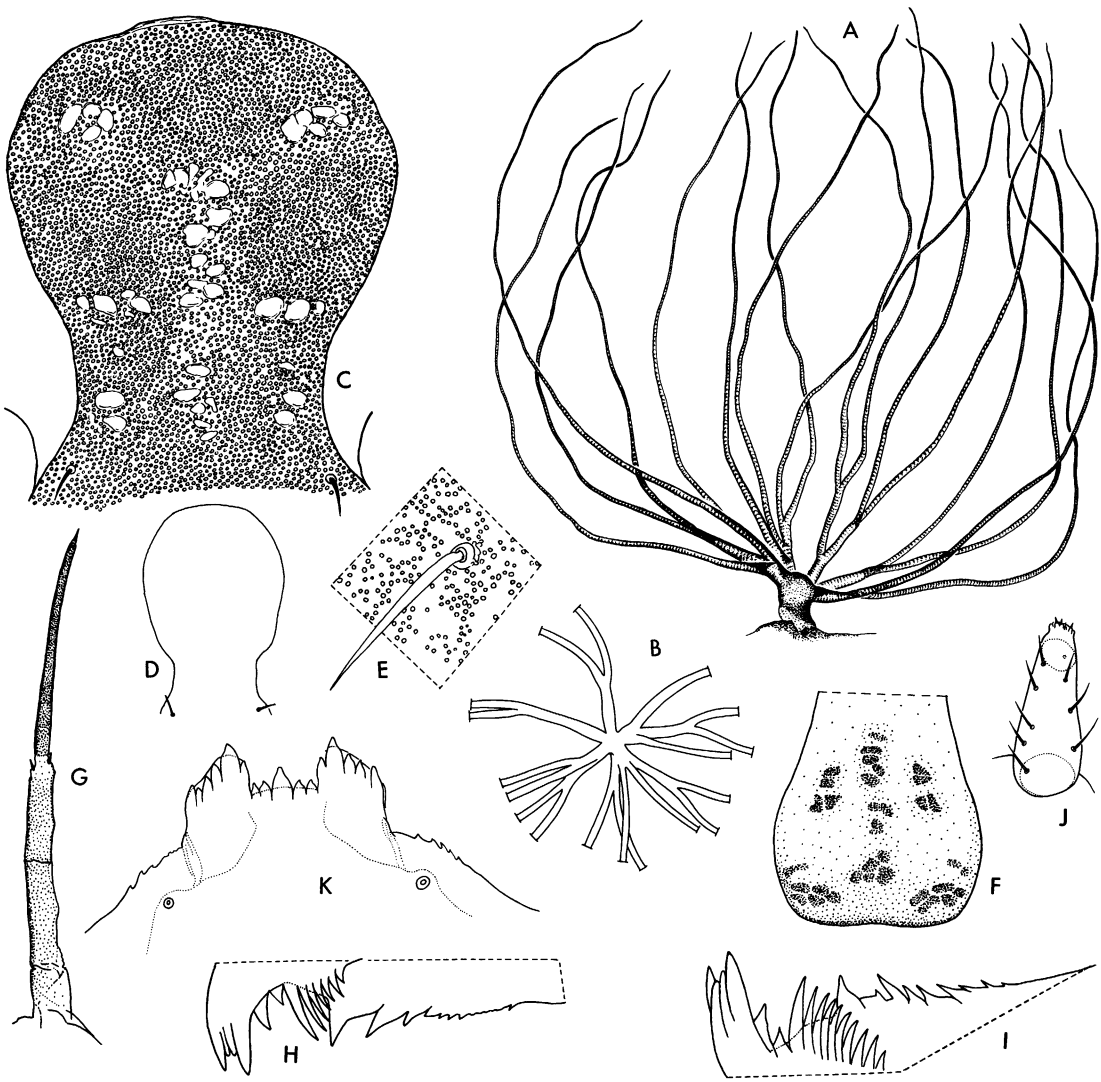

Fig. 58. *G. luispenai.* A–E. Pupa. **A.** Gill. **B.** Base of gill, frontal view. **C.** Frontoclypeus of male. **D.** Outline of frontoclypeus of male. **E.** Portion of thorax, with platelets and trichome. F–K. Larva. **F.** Cephalic apotome. **G.** Antenna. **H, I.** Apex of mandible. **J.** Maxillary palp. **K.** Teeth of hypostomium.

eyes dark brown at location of large facets and black in the area of small facets. Antenna, maxillary palp, and clypeus grayish brown; scapus and pedicellus somewhat reddish. Setae of occiput, interocular space, clypeus, and maxillary palp from light castaneous to dark. Scutum, scutellum, metanotum, and pleura dark grayish brown; pleura and metanotum pollinose. Setae of scutum and scutellum brass-gray, legs brown, with articulations and tarsi darker and hairs dark brown. Wing and abdomen as in female. Shape and proportions of antennal articles as in figure 57K. Maxillary palp (fig. 57L) with length of second article less than half that of distal one, as in female. Sensory vesicle (fig. 57M) smaller to half the diameter of the article. Shape, proportions, and pigmentation of the middle and hind leg articles as in figure 57N, O. Posterior basitarsus with ratio length to width 6.0–6.5. Calcipala longer than half of second tarsomere (fig. 57P). Genitalia very similar

to those of *brophyi.* Distimere with two apical hooks (fig. 57Q). Basal plate as shown in figure 57R.

Pupa. General aspect very similar to that of *marginalis,* as are the aspect and structure of cocoon. Length of cocoon 4.5–5.0 mm. Length of pupa 4.0–4.5 mm; cephalopterothecal length 2.3–2.6 mm; length of gills measured in lateral aspect 2.0–2.3 mm; measurements laterally 2.0–2.3 mm. Cocoon occasionally covering base of gills. Number and arrangement of filaments in lateral view very similar to that of *marginalis* but in dorsal view the filaments arranged in more definite groups, with only five primary branches (fig. 58A, B). Color of these filaments grayish brown, darker than in *marginalis.* Frontoclypeus of female and male as shown in figure 58C, D. Head, thorax, and abdomen with well-developed platelets; anteriorly the number of platelets approximately twice that in *marginalis.* Platelets and trichomes of thorax as shown in figure 58E. Chaetotaxy, thorax, and abdomen as in *brophyi.*

Larva. Length 6.5–6.8 mm; width of head 0.6 mm. General aspect of body as in *brophyi.* Color of body pale grayish brown; of the head light brown, lighter than in *marginalis.* Cephalic apotome (fig. 58F) very similar to that of *antarcticus,* showing the dark spots very distinctly. Antenna below level of stem apex of cephalic fan. Ratio of antennal articles I–III = 1:1.06:1.5. First article apparently subdivided near base (fig. 58G). Terminal sensillum about 3.5 times as long as wide. Cephalic fan with 36 to 41 rays. Dentition of mandible with 7–10 internal teeth (fig. 58H, I). Maxillary palp as shown in figure 58J. Dentition of hypostomium on its anterior border as in figure 58K, with 3–4 setae on each side. Gill histoblast very similar to that of *marginalis.* Anal disc as in *brophyi,* with approximately 76 rows of 17 hooks each.

HOLOTYPE: CHILE: *Coquimbo:* Hacienda Illapel, 1200 m, Oct. 21, 1967 (S. Coscarón; AMNH), female.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 male allotype, 6 females, 2 males, paratypes, reared, various larvae and pupae; 5 females, 3 male paratypes, reared, larvae and pupae (MLP). CHILE: *Coquimbo:* El Calabozo, Hacienda Illapel, 1400 m, Oct. 22, 1967 (S. Coscarón; AMNH), various larvae and pupae; Hacienda Illapel, Nov. 1–6, 1954 (L. Pena; CNC), 1 male; stream at the edge of International Highway, 2500 m, Oct. 24, 1967 (S. Coscarón; AMNH), various larvae; Los Veroles, 40 km N Los Vilos, July 2, 1966 (Irwin-Hickins; CIS), 3 females; Combarbala, Moquehua, Majada Blanca, Aug. 2, 1960 (L. Pena; CNC), 2 females; Cuesta Canela Baja, Oct. 23, 1961 (L. Pena; CNC), 1 female; Rio Caren-Caren, Hacienda Illapel, 880 m, Nov. 13, 1963 (G. F. Edmunds; CNC), 1 pupa and various larvae.

ETYMOLOGY: Named for Señor Luis Peña, famous collector of South American insects.

BIOLOGY: This species was collected on aquatic plants in clear streams with rather large volumes (larger than for *marginalis*). In some places it was found together with *Simulium (P.) stelliferum.* Temperature of streams was relatively warm, approximately 15°C.

DISCUSSION: This species is very close to *marginalis*; morphological differences are given under the discussion of that species. *G. marginalis* occupies a more northern area and a somewhat higher altitude.

Gigantodax chilensis (Philippi)

Figures 59A–Y, 60A–G, 61A–U, 178C

Simulium chilense Philippi, 1865: 634. Pinto, 1931: 728. Vargas, 1945: 126.

S. (Gigantodax) chilense: Edwards, 1931: 139. Orfila, 1935: 1528.

Gigantodax chilense: Wygodzinsky, 1961a: 460; 1961b: 564. Vulcano, 1967: 3; 1977: 290. [Incorrect gender]

S. (Gigantodax) rufinotum Edwards, 1931: 140. NEW SYNONYMY.

DIAGNOSIS: Adults small, yellowish brown, calcipala surpassing second tarsomere, wing membrane fumose, and pupal gills arranged treelike with a tendency to join each other apically.

REDESCRIPTION: *Female.* Wing length 3.3–4.0 mm. Head black, eyes black, antenna light colored at base; flagellum, frons, clypeus, and maxillary palp dark grayish-brown; frons and clypeus with silvery pollinosity. Pilosity of the frons, occiput, clypeus, and maxillary palp from silvery to golden.

Scutum and scutellum yellowish brown, with metanotum dark brown and gray pol-

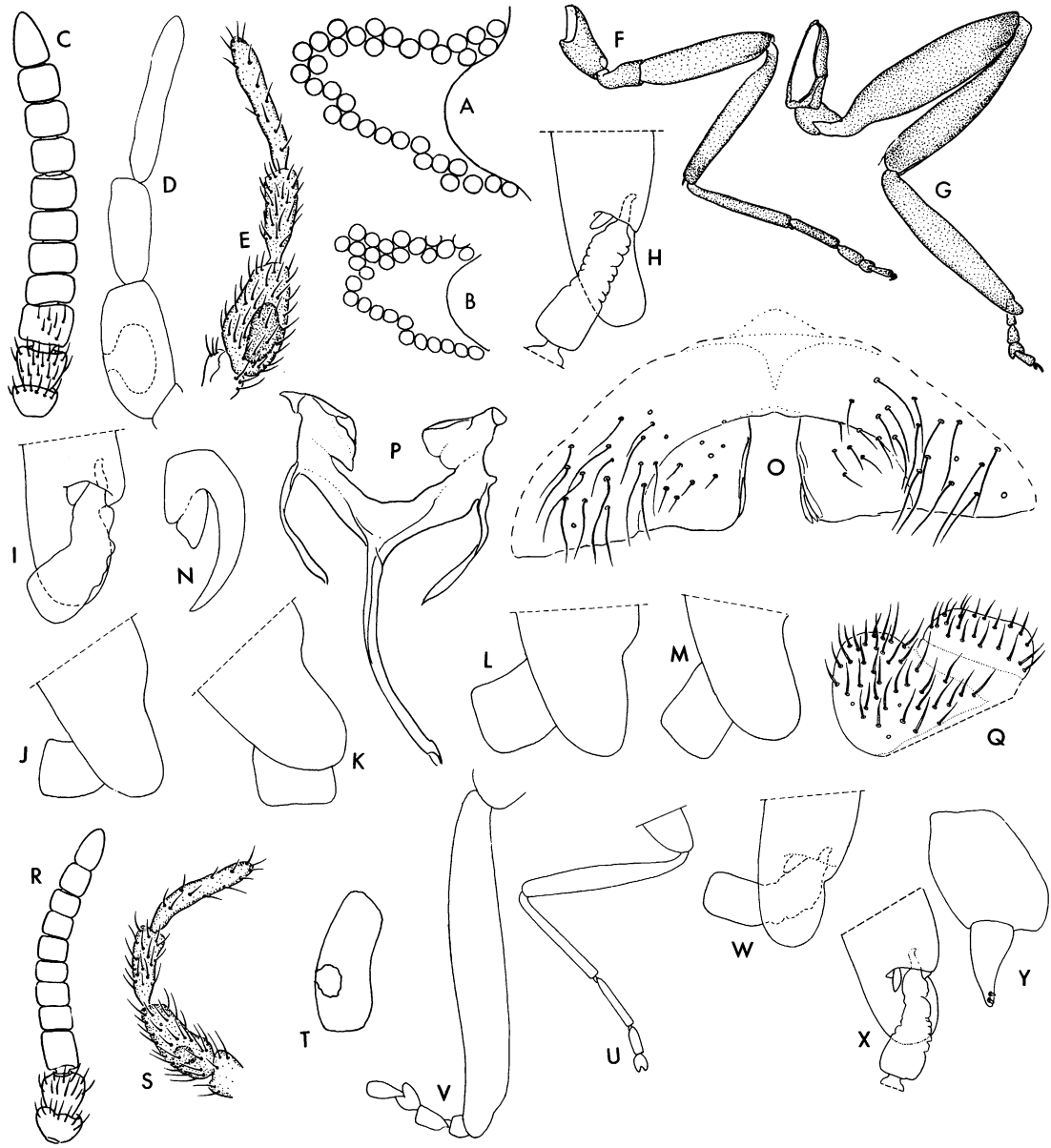

Fig. 59. *Gigantodax chilensis.* A–P. Female. **A, B.** Fronto-ocular triangle. **C.** Antenna of female. **D.** Maxillary palp, Corral. **E.** Same, Lago Frio. **F, G.** Fore and hind leg. **H–M.** Calcipala, with second tarsal segment (H, M. Lago Frio, I. Corral, J. Temuco, K. Isla de los Estados, L. Bariloche). **N.** Claw. **O.** Eighth sternite of female, with gonapophyses. **P.** Genital fork. **Q.** Cercus and paraproct. R–Y. Male. **R.** Antenna. **S.** Maxillary palp. **T.** Second segment of maxillary palp. **U.** Foreleg. **V.** Posterior basitarsus, with remaining tarsal segments. **W, X.** Calcipala, with second tarsal segment. **Y.** Basimere and distimere.

linosity as on the pleura. The scutum under certain illumination shows a median longitudinal stripe approximately as wide as one-third of the total width and darker than the remainder. Pilosity of scutum and scutellum from yellowish brown to golden; depending on illumination, from brown to grayish brown. Legs and wing veins yellowish brown

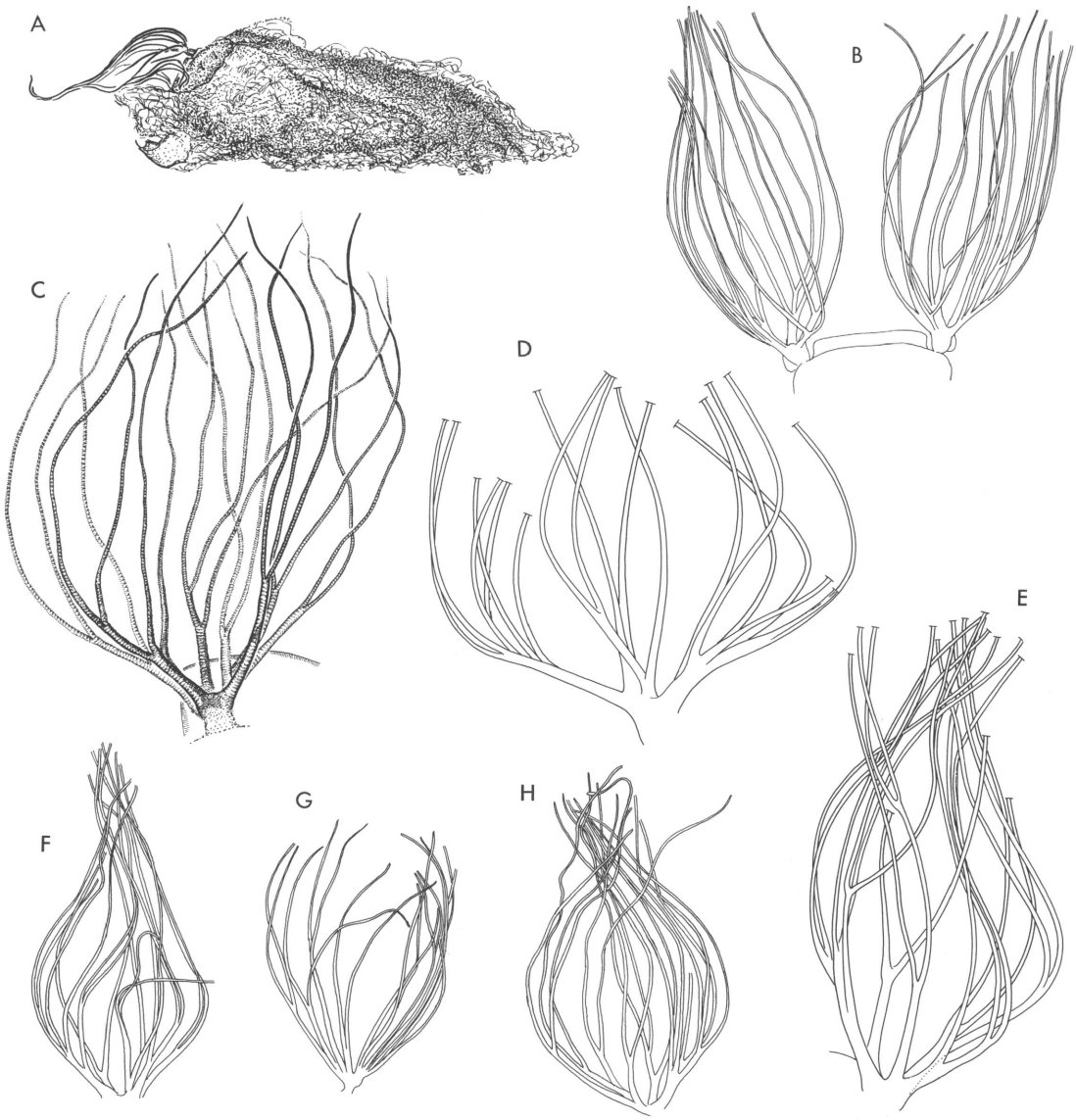

Fig. 60. *G. chilensis.* Pupa. **A.** In cocoon, lateral aspect. **B–H.** Gills (B. Temuco, C. Chonchi, D. Isla de los Estados, E, F. Corral, G. Chorillo Alicia).

to dark brown, somewhat darker than scutum and with brown to light grayish brown hairs. Wing membrane smoky. Abdomen dark chestnut brown with the distal margins of the tergites lighter; hairs pale brown colored.

Frons with median sulcus. Fronto-ocular triangle longer than wide (fig. 59A, B). Shape and proportion of antennal segments as in figure 59C. Maxillary palp with apical segment less than twice the penultimate (fig. 59D, E); ratio length/width of second segment = 1:0.63–0.68. Structure of sensory vesicle as in *antarcticus.* Maxilla with about 30 teeth and mandible with 24. Hairs of scutum and scutellum as in *brophyi.* Wing chetotaxy as in *brophyi,* but with one or two spines in the distal fourth of R_1. Shape and proportions of the segments of the fore and hind leg as shown

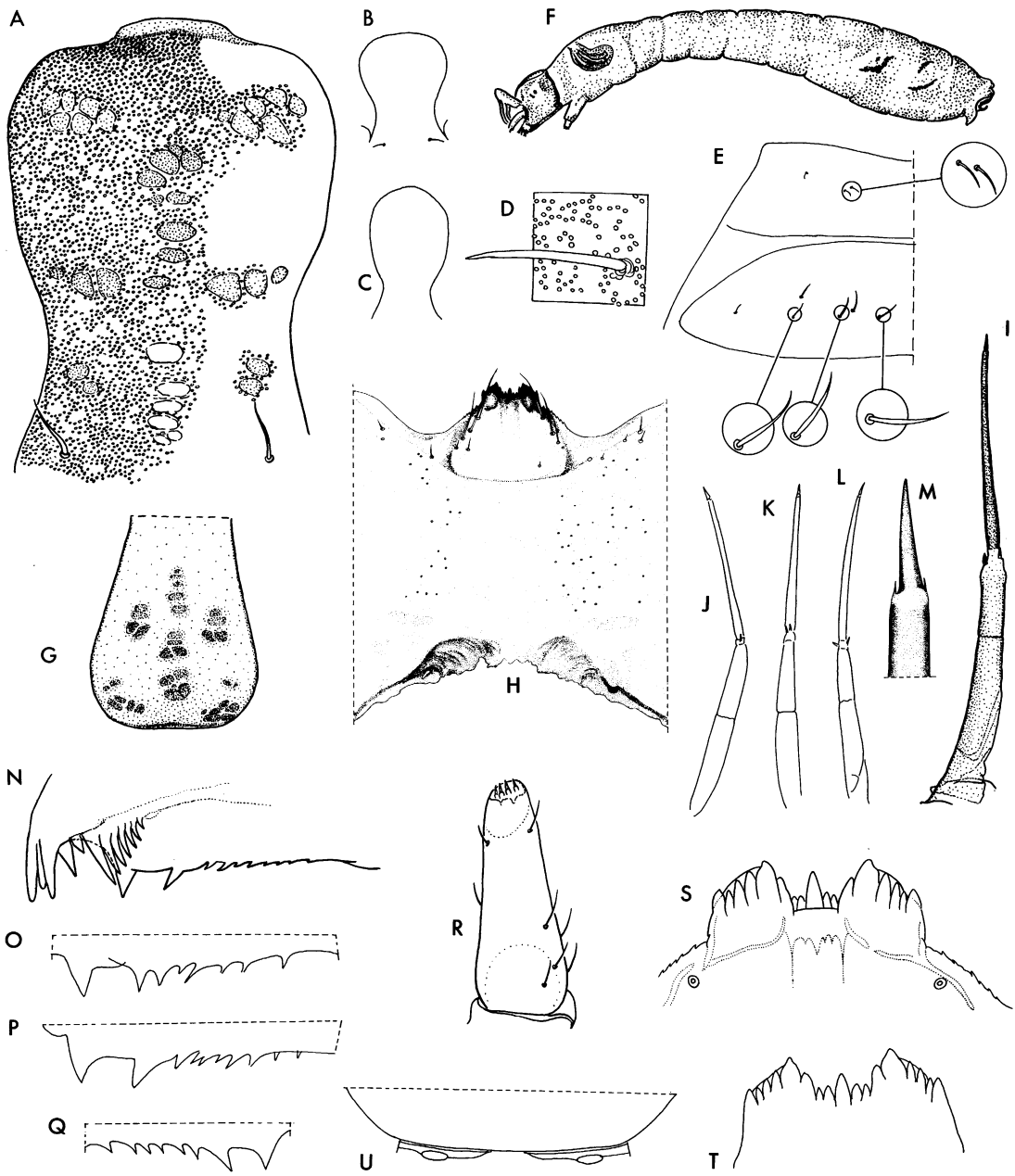

Fig. 61. *G. chilensis.* Pupa. **A.** Frontoclypeus of female. **B, C.** Outline of female and male frontoclypeus (B. Temuco, C. Chonchi.) **D.** Seta of thorax. **E.** Chaetotaxy of I and II abdominal tergite. **F.** Larva, lateral view. G–T. Larva. **G.** Cephalic apotome. **H.** Hypostomial bridge. **I, J–L.** Antennae. **N.** Apex of mandible. **O–Q.** Mandibular serration. **R.** Maxillary palp. **S, T.** Teeth of hypostomium. **U.** Cervical sclerites.

in figure 59F, G. Calcipala longer than wide, almost attaining the end of the second posterior tarsal segment (fig. 59H–M); claws as shown in figures 59N, 178C. Sternite VIII and gonapophyses as in figure 59O; sternite VIII with 20 to 25 setae. Genital fork, para-

procts, and cercus as illustrated in figure 59P, Q. Cercus rather flat. Spermatheca as in *brophyi.*

Male. Holoptic. Length of wing 3.2–3.3 mm. Antenna, maxillary palp, and clypeus grayish brown. Hairs, antenna, maxillary palp, clypeus, interocular area, and occiput from light grayish brown to dark chestnut brown according to illumination. Scutum and scutellum orange yellow and light brown. Pleuron, metanotum, legs, and wing venation light brown; wing membrane smoky. Shape and proportion of antennal articles as in figure 59R. Maxillary palp as in figure 59S, diameter of sensory vesicle one-half of basal article (fig. 59T), structure of sensory vesicle as in *antarcticus.* Wing as in the female, but spines of R_1 less visible. Shape, proportion of some segments of foreleg as shown in figure 59U. Basitarsus of hind leg about five times as long as wide (fig. 59V). Calcipala longer than wide, and almost attaining posterior border of the tarsomere 2 (fig. 59W, X). Basimere and distimere as figure 59Y. Genitalia very similar to those of *antarcticus.*

Pupa. Cocoon with irregular fabric (fig. 60A). Brown color also in a large part of the gills. Tissue of the cocoon coarse and thick with the details of the tissue visible. Total length of cocoon 5.0–5.5 mm. Length of body 3.0–3.5 mm. Length of the respiratory organ 1.3–1.5 mm. Gill treelike, with branches arranged in a basketlike shape sometimes joined to each other, especially in apical region (fig. 60B–H). Five primary branches arising from a short trunk. The distance of the secondary and tertiary subdivisions vary in different specimens. This species shows subdivision at the greatest distance from the base of all southern species studied that have 18 branches.

Head and thorax light brown with conspicuous platelets, especially on the frons and the anterior dorsal portion of the thorax. Frontoclypeus shape as shown in figure 61A–C. Platelets of frontoclypeus abundant (fig. 61A). Chaetotaxy of thorax and abdomen as in *antarcticus.* Setae and platelets of thorax as in figure 61D. Setae of abdominal tergites I–II as in figure 61E.

Larva. Maximum length 6.5 mm. Width of head 0.65 mm. Body pale grayish brown. Head yellowish brown. Shape of body as in figure 61F. Cephalic apotome with short setae and ornamented as in figure 61G. Hypostomial bridge with homogeneous coloration (fig. 61H). Antenna somewhat shorter than stem of cephalic fan. Antenna as in illustrations (fig. 61I–L). Ratio of segments I–III = 1:0.5–0.7:1.4–1.7. Terminal sensillum 4.5 times as long as wide at base (fig. 61M). Cephalic fan with approximately 35 rays. Dentititon of the mandible as in figure 61N–Q, with 7–9 inner teeth and 8–10 marginal serrations. Maxillary palp as in figure 61R. General aspect of hypostomium much as in *antarcticus.* Anterior margin showing the corner teeth comparatively short (fig. 61S, T), and only with four setae on each side. Cervical sclerites as in figure 61U. Sclerite of proleg with about 26 teeth. Histoblast very similar to that of *antarcticus.* Anal disc with 82–96 rows of hooks consisting of 15–18 hooks each.

BIOLOGY: This species was collected in clean, not very cold and slow-flowing water and generally on water plants. It is frequently found together with *marginalis*; in Chiloe (Huillinco) with *Paraustrosimulium anthracinum.*

MATERIAL EXAMINED: ARGENTINA: *Tierra del Fuego:* Isla de los Estados, Nov. 26, 1967 (A. Bachmann; MLP), 1 female reared (with the associated pupal exuviae), pupae and larvae; Isla de los Estados, San Juan, May 12–15, 1971 (Flint and Hevel; USNM), 3 females; Isla de los Estados, Puerto Cook, May 16–19, 1971 (Flint and Hevel; USNM), 2 females. *Chubut:* Puerto Limonao, Lago Futalaufquen, Jan. 14, 1962 (S. Coscarón; MLP), 1 male with the associated exuviae; Lago Puelo, Nov. 1950 (P. Wygodzinsky; AMNH), 1 female. *Rio Negro:* Near Hotel Tronador, Jan. 18, 1983 (S. Coscarón; MLP), pupae; Lago Mascardi, April 11, 1983 (S. Coscarón; MLP), pupae and larvae; Lago Frias, Feb. 13, 1967 (S. Coscarón; AMNH), 3 males, 4 females associated with the corresponding pupal exuviae, pupae; Bariloche, Nov. 23, 1950 (P. Wygodzinsky; AMNH), 2 males, 1 female associated with corresponding pupal exuviae, pupae; Bariloche, Nov. 26, 1950 (P. Wygodzinsky; AMNH), 1 male, 1 female associated with the corresponding pupal exuviae; Bariloche, Nov. 27, 1950 (P. Wygodzinsky; AMNH), pupae; Bariloche,

Colonia Suiza, Sept. 27, 1975 (S. Coscarón; MLP), pupae; Cerro Catedral, Nov. 25, 1950 (P. Wygodzinsky; AMNH), pupa; Bariloche (Shannon), Nov. 3, 1926: 1 male; Nov. 28–30, 1926, 1 male; Dec. 16, 1926, 1 female; Nov. 6, 1926, 1 female (as paratypes of *G. rufinotum* Edwards in AMNH); Bariloche (Shannon), Nov. 5–10, 1926, 1 male; Nov. 1926, 1 male (paratypes of *G. rufinotum* Edwards in USNM); Bariloche (Shannon), 1 male (det. *S. (G.) chilense* by Edwards in USNM). Valcheta, Arroyo Valcheta, March 13, 1973 (S. Coscarón; MLP), pupae and larvae, female and male pharate. *Neuquen:* 30 km NE of Bariloche, Oct. 22, 1970 (S. Coscarón; MLP), 1 male (associated with the corresponding pupal exuviae), pupae; Valle Encantado, Oct. 21, 1970 (S. Coscarón; MLP), 1 male (associated with the corresponding pupal exuviae, pupae; Confluencia, Oct. 25, 1970 (S. Coscarón; MLP), pupae; La Lipela, Jan. 24, 1971 (S. Coscarón; MLP), pupae; Arroyito, 10 km SE de San Martin de los Andes, 960 m, Oct. 22, 1970 (S. Coscarón; MLP), pupae; Pucara, Feb. 20, 1967 (S. Coscarón; AMNH), pupae; Pucara, Oct. 21, 1970 (S. Coscarón; MLP), pupae; Arroyo Hua-Hum, Jan. 29, 1979 (S. Coscarón; MLP), 6 pupae; Hua-Hum (S. Coscarón; MLP), Jan. 23, 1980, pupae; Base del Cerro Chapelco, Jan. 21, 1978 (S. Coscarón; MLP), pupae and larvae; Arroyo Quilanlahue, Jan. 22, 1978 (S. Coscarón; MLP), 5 pupae; Nov. 8/14, 1982, 5 females, 2 males; Jan. 8, 1983, 2 females; Jan. 6, Aug. 5, 1982; Apr. 4, 1983 (Gentili; MLP), several larvae; creek near Arroyo Partido, Jan. 23, 1978 (S. Coscarón; MLP), several pupae and larvae; Arroyo Quiltrahue, Jan. 8, Jan. 28, Feb. 20, Apr. 1, July 7, Nov. 15, 1979; Jan. 8, Apr. 30, Dec. 21, 1980; Nov. 10, 1981; Dec. 10, Jan. 7, Mar. 3, Apr. 3, May 4, June 4, Aug. 4, Nov. 28, 1982; Jan. 2, Feb. 7, 28, Apr. 4, May 1, June 3, July 2, 1983 (Gentili; MLP), abundant pupae and larvae; Arroyo Yuco, Jan. 29, 1979 (S. Coscarón; MLP), abundant pupae and larvae; Jan. 23, 1980 (S. Coscarón; MLP), pupae and larvae; Puesto Chiridiale, Jan. 23, 1980 (S. Coscarón; MLP), 1 pupa and larvae; Apr. 30, 1980 (Gentili; MLP), larvae; Arroyo de la Telesilla, July 3, 1982 (Gentili; MLP), larvae; San Martin de los Andes, Sept. 24, 1981, 3 males, Sept. 9/Oct. 5, 1982, 2 females (Gentili; MLP); Quilahuinto, 1000 m, Oct. 4, 1980 (Gentili; MLP), 1 female, 2 males; Alumine-Purime, 1200 m, Jan. 3, 1978 (Gentili; MLP), 1 female, 1 male. CHILE: *Magallanes:* Isla Wellington, Pto. Charrua, Nov. 20–26, 1969 (O. Flint; USNM), 2 females; Puerto Eden, Nov. 23, 1969 (O. Flint; USNM), 1 female; *Aysen:* Rio Cisnes, Feb. 1961 (L. Pena; CNC), 7 females; Puerto Cisnes, Feb. 1–15, 1961 (L. Pena; CNC), 23 females; Puerto Aysen, Jan. 24–26, 1961 (L. Pena; CNC), 2 females; Lago Frio, Colhaique, Valle Rio Simpson, Jan. 17–20, 1961 (L. Pena; CNC), 3 females; Puerto Cristal, Lago Buenos Aires, Jan. 22, 1956 (Kuschel), 1 female, 1 male; Balmaceda, Jan. 17–20, 1961 (L. Pena; CNC), 4 females; *Chiloe:* Melinka, Archipielago de los Chonos, Jan. 28–31, 1962 (L. Pena; CNC), 1 male; Dalcahue, Jan. 17–22, 1962 (L. Pena; CNC), 17 females, 1 male; Chonchi, Feb. 7, 1967 (S. Coscarón; AMNH), 6 females, 3 males (associated with the corresponding pupal exuviae), pupae; Huillinco, Feb. 7, 1967 (S. Coscarón; AMNH), 4 females (associated with the corresponding pupal exuviae), pupae; 3 km NE of Huillinco, Feb. 7, 1967 (S. Coscarón; AMNH), 1 female, 5 males (associated with the corresponding pupal exuviae), pupae; *Llanquihue:* Frutillar, Sept. 16, 1957 (Kuschel), 1 male; 8 km W of Puerto Varas, Jan. 16–31 (Ross and Michelbacher; CAS), 3 males; Osorno, Termas de Puyehue, Feb. 4, 1967 (S. Coscarón; AMNH), 1 male (associated with the corresponding pupal exuvia), pupae; *Valdivia:* between Valdivia and Paillaco, Feb. 4, 1967 (S. Coscarón; AMNH), pupae; Brazo de Llollehue, Puente Itropulli, W of Ranco, Feb. 4, 1967 (S. Coscarón; AMNH), pupae; Corral, Arroyo La Marina, Feb. 3, 1967 (S. Coscarón; AMNH), pupae; Paillaco, Feb. 4, 1967 (S. Coscarón; AMNH), pupae; *Cautin:* between Pucon and Villarrica, Feb. 2, 1967 (S. Coscarón; AMNH), pupae; between Temuco and Freire, Feb. 1, 1967 (S. Coscarón; AMNH), 1 female pharate and pupae; *Malleco:* Termas del rio Blanco, 1080 m, Jan. 22, 1967 (Irwin and Stange; Riverside), 1 female; Gualletue, Dec. 9–14, 1963, 1200 m (L. Pena; CNC), 1 female; Sierra de Nahuelbuta, W of Angol, 1200 m, Jan. 3, 1951 (Ross and Michelbacher; CAS), 1 female; *Bio-Bio:* El Abanico, Dec. 30, 1950 (Ross and Michelbacher; CAS), 1 female;

Concepcion: Escuadron, Oct. 13–19, 1972 (S. Coscarón; AMNH and MLP), 3 females, 3 males with exuviae; Quebrada Honda, 15 km N of Concepcion, Oct. 12, 1972 (S. Coscarón; AMNH and MLP), 3 males, 2 females (associated with the corresponding pupal exuviae); Rinconada de Curcura, 3 km S of Lota, Oct. 12, 1972 (S. Coscarón; AMNH), 1 male (with the corresponding pupal exuviae); Laraquete, Oct. 13, 1972 (S. Coscarón; MLP), pupae; *Nuble:* 40 km W of San Carlos (Ross and Michelbacher; CAS), 2 females, 1 male; *Maule:* Puente La Madera, on creek 20 km of Cauquenes, Jan. 30, 1967 (S. Coscarón; AMNH), pupae; *Curico:* Estero La Junta, Jan. 1964 (L. Pena; CNC), 3 females; Cajon del Rio Claro, SE of Los Quenes, Oct. 9, 1966 (Schlinger; CIS), 2 males; *Santiago:* 4 km SW of Caleu, Oct. 11, 1972 (L. Pena and P. Wygodzinsky; AMNH), pupae; *Coquimbo:* Los Vilos, Oct. 22, 1967 (S. Coscarón; AMNH), pupae.

DISCUSSION: The probable type is a female deposited in Museo Nacional de Historia Natural of Santiago, Chile, with one label "Corral 1859" and another "Philippi." The specimen is not well preserved but is recognizable. Our material agrees with this specimen and Edwards's description, but the pupal gill illustrations of that author were mislabeled: *chilensis* should be *marginalis,* and *fulvescens* should be *chilensis.*

The species closest to *chilensis* is *fulvescens,* but it is possible to differentiate the two by the following characters in the latter species: imagos lighter yellow, pupal gill flattened frontally, and larvae with submentum ornamented with a median longitudinal light band.

Dark imagos of *chilensis* are close to some *marginalis* specimens; hyaline wings, and shorter calcipala are small differences, but the disposition of pupal gill branches in *marginalis* help to easily distinguish the two species. Dark imagos of *chilensis* could confuse it with *araucanius,* but the hooklike shape of the subbasal claw tooth, more abundant spines, R_1, and the 11 pupal gill branches permit easy separation.

The pupal gill of *chilensis* differentiates the species from similar ones with 18 branches by the subdivision of the primary branches at a greater distance from the base.

We have examined the male holotype of *Gigantodax rufinotum* kept in the British Museum (Nat. Hist.): two males and one female, paratypes of AMNH, and two males, paratypes of USNM. Edwards (1931) already suggested that this might be "only a form of *chilense.*" We agree with this hypothesis because the color pattern of *rufinotum* falls within the range of variation of *chilensis,* and there are no morphological characters to distinguish the two species.

Gigantodax flabellus, new species

Figures 62A–S, 63A–G

DIAGNOSIS: *Gigantodax flabellus* differs from other species close to *G. ortizi* by the fanlike structure of the pupal gills.

DESCRIPTION: *Pharate female.* Color not known. Frontal angle 45°. Antenna not examined. Fronto-ocular triangle (fig. 62A) higher than wide. Mandible with teeth on inner margin only. Maxilla with normal teeth. Last segment of maxillary palpi 1.5 times as long as penultimate (fig. 62J). Second segment of maxillary palp elongate suboval, ratio length/width 1:2.0–2.4. Sensory vesicle oval, elongate, with distinct short neck (fig. 62D). Wing not examined. Calcipala extending beyond middle of second tarsomere (fig. 62O). Basal tooth of claws similar as in *ortizi.* Genitalia not examined in detail; spermatheca as in *ortizi.*

Pharate male. Color not known. Holoptic. Shape and proportions of antennal segments as in figure 62B; ratio length/width of first flagellomere 1:0.53–0.58. Last segment of maxillary palp as in female (fig. 62C). Sensory vesicle small, suboval, with distinct neck (fig. 62E–G). Wing not examined in detail, apparently similar to those of related species; spinules present on R_1. Shape and proportions of some leg segments as in figure 62I. Fore basitarsus 13.6 times as long as wide; hind basitarsus not measured. Calcipala extending close to apex of second tarsomere (fig. 62P). Genitalia as in *ortizi.*

Pupa. Cocoon irregularly slipper shaped, completely covering body of pupa, including in some specimens, the base of the gills (fig. 63A). Fabric of cocoon consisting of loosely woven irregular mesh of fine and coarse threads, with very small apertures; color of

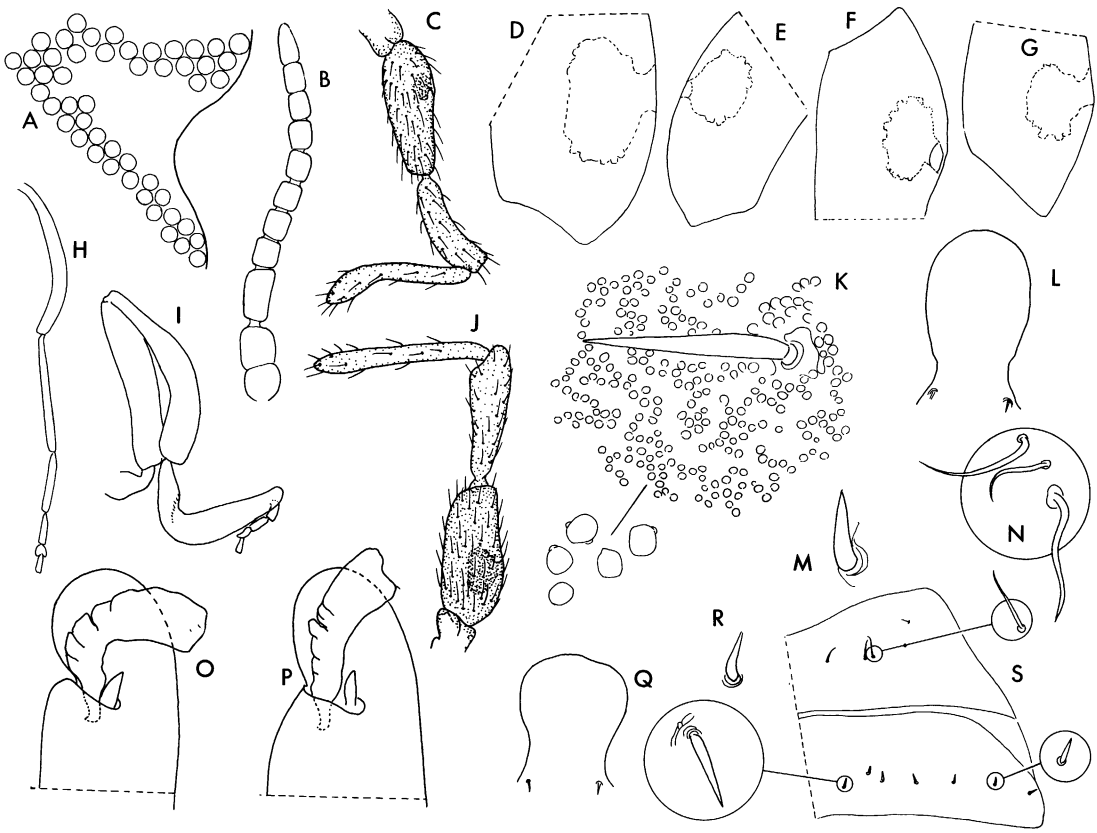

Fig. 62. *Gigantodax flabellus.* **A.** Fronto-ocular triangle. **B.** Antenna of male. **C.** Maxillary palp of male. D–G. Second article of maxillary palp, with sensory vesicle. **D.** Female. **E–G.** Male. **H.** Foreleg of male. **I.** Hind leg of male. **J.** Maxillary palp of female. **K.** Lower dorsocentral trichome of thorax of pupa, with platelets. **L.** Frontoclypeus of male of pupa. **M.** Hook of abdominal tergite III of pupa. **N.** Setae of apical portion of abdomen. **O.** Calcipalal with second tarsal segment, male. **P.** Same, female. **Q.** Frontoclypeus of female pupa. **R.** Dorsolateral seta of tergite IV. **S.** Chaetotaxy of abdominal tergites I and II.

strands light brown. Cocoon encrusted with tiny organic and inorganic particles. Length of cocoon approximately 5.0 mm. Total length of body of pupa 3.5 mm; cephalopterothecal length 2.5 mm. Gills light brown, with filiform forwardly directed branches. Stalk of gills very short, 1.5 times as long as wide on narrow portion. Gill (fig. 63B–E, G) with branches considerably diverging at base, interlacing apically, forming a fanlike structure parallel to sagittal plane of body of pupa; this fanlike structure somewhat concave mesially, especially on lower half of gill. Four primary branches very short, secondary filiform branches arising dichotomously at very short distance from base of branched portion of gill. Total length of intact gill 3 mm. Surface structure of gill branches as in *ortizi.* Shape and proportion of frontoclypeus of male and female as in figure 62L, Q. Platelets of frontoclypeus (fig. 63F) and thorax (fig. 62K) from smooth to faintly verrucose, very numerous. Facial trichomes short, spinelike. Dorsocentral trichomes of thorax consisting of two stout spinelike setae, and one strong hairlike seta (fig. 62R). Dorsolateral trichomes in shape of very delicate, long hairs. Setae of abdominal tergite I (fig. 62S) strong, hairlike, length 50–70 μm (rarely 90 μm); setae of tergite II short and stout, length 22–35 μm. Tergites III and IV each with 4 + 4 short hooks (fig. 62M); anterodorsal setae in shape

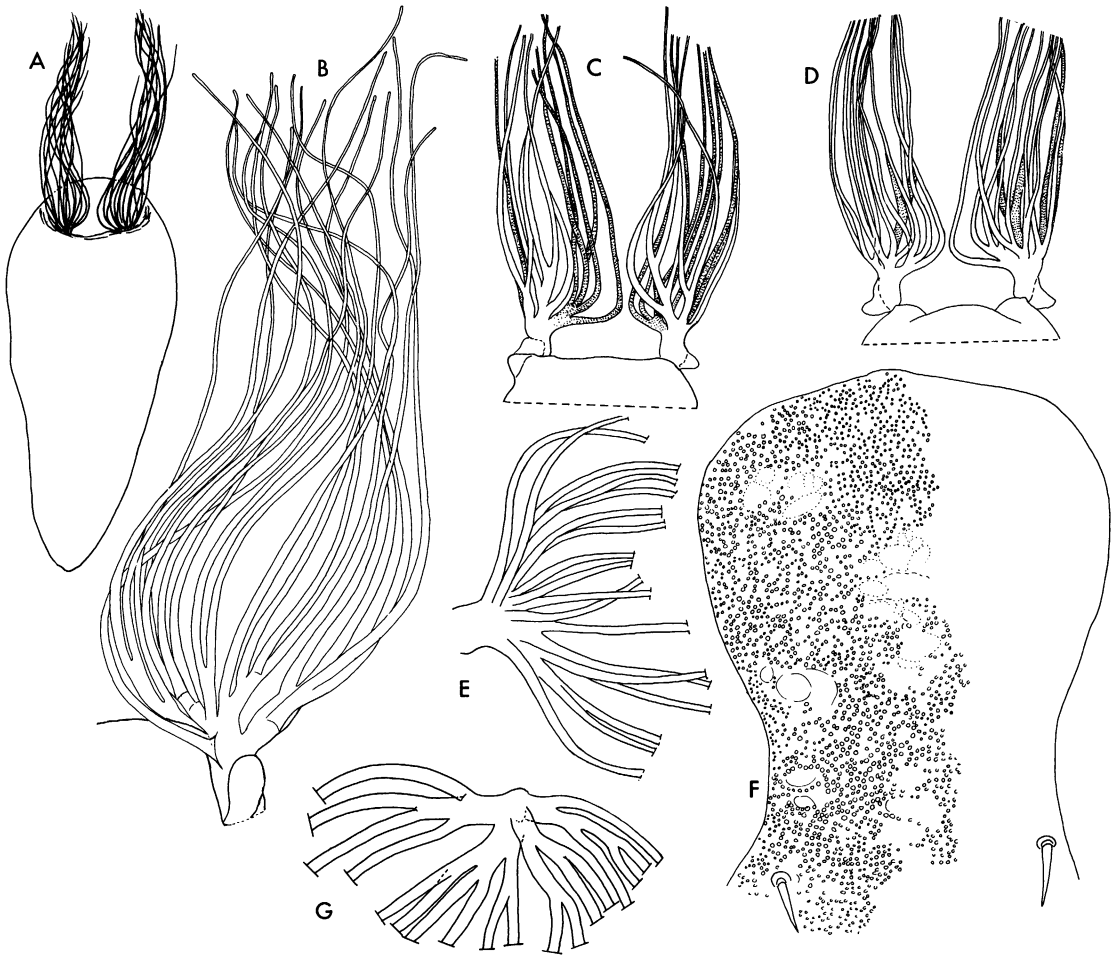

Fig. 63. *G. flabellus.* Pupa. **A.** Pupa in cocoon, dorsal view. **B.** Pupal gill. **C.** Anterior portion of body of pupa, under surface. **D.** Same, dorsal surface. **E.** Base of pupal gill. **F.** Frontoclypeus. **G.** Basal portion of gill.

of small short spine, shorter than hooks. Setae of tergites VI–VIII, continuous or with short interruptions, consisting on tergite VII of 37–42 spines, length 25–40 μm, viz., about as long as setae of this segment. Specialized setae of segments VIII and IX from straight to variously curved, no branched setae observed (fig. 62N). Sternite VIII glabrous. Sternite IV with small spine- or hooklike setae arranged in pairs and singly. Sternite V with 3 + 3, sternal plates VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VIII. Sternite VIII glabrous.

Larva. Unknown.

HOLOTYPE: ECUADOR: *Pichincha:* road from Quito to Papallacta, 3300 m, July 20–Aug. 9, 1969 (P. and B. Wygodzinsky; AMNH), pharate male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, one pharate female, allotype, one pharate male, paratype (all reared and with their associated pupal exuviae), pupae. VENEZUELA: *Merida:* road from Apartaderos to Santo Domingo, 2600 m, Feb. 16–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 pupa.

ETYMOLOGY: Name taken from the Latin *flabellum,* a fan, in reference to the shape of the gills of the pupa.

BIOLOGY: This species was collected in Ecuador in a small, cold (9.5°C) irrigation ditch in open land, with clear water but with considerable amounts of organic debris deposited on the substrate. We have no data regarding the substrate from which the pupa was taken; pupae of other species of *Gigantodax* collected here were taken from vegetation, and both the upper and undersurfaces of large stones.

DISCUSSION: *G. flabellus* and *G. awa* are very closely related and seem to have affinities to *ortizi* and its allies. The more open, fanlike arrangement of the gill filaments and the very short gill stalks found in *flabellus* and *awa* probably represent the plesiomorphic condition of the group as a whole. *G. multituberculatus* is somewhat intermediate, with its dorsal inner primary branches conspicuously diverging from the remaining.

Gigantodax awa, new species
Figure 64A–U

DIAGNOSIS: *Gigantodax awa* differs from the most closely related species, *flabellus,* by slight differences in measurements and structure as discussed below.

DESCRIPTION: *Pharate female.* Color of scutum light orange (but not necessarily so in fully developed imago). Frontal angle approximately 45°. Fronto-ocular triangle (fig. 64C) higher than wide. Shape and proportions of antennal segments as shown in figure 64J. Mandible with teeth on inner margin only, approximately 20 present. Maxilla with 28 teeth. Maxillary palp as in figure 64A; its distal segment 1.5 times as long as penultimate. Second segment very slender and elongate, inverse claviform, ratio length/width 1: 0.33. Sensory vesicle oval (fig. 64B), with distinct neck. Wings not examined. Shape and proportions of some leg segments as in figure 64G, H. Calcipala extending much beyond middle of second tarsomere. Basal tooth of claw as in figure 64P. Genitalia without special characters; genital fork and gonapophyses as shown in figure 64D, O.

Male. Length of wing 4.2 mm or more. Scutum bright orange; scutellum and metanotum light brown, metanotum with strong purple tinge on anterior half. Pleura light brown. Adpressed setae of thorax yellow, large erect setae dark. Leg and halteres light brown. Wing veins dark brown; setae of stem vein and of remaining veins dark. Abdominal tergites from velvety piceous to black, their posterior border narrowly whitish. Setae of abdominal fringe and remaining abdominal hairs golden colored.

Holoptic. Antenna and maxillary palp much as in female; sensory vesicle (fig. 64E) rather large, oval. Wing with Sc bearing 23 hairs. R with setae arranged in two irregular rows. R_1 with setae in one or two irregular rows; spinules present, beginning halfway between r-m crossvein and level of insertion of Sc on C. R_s with setae in one row on apical portion, in two or three irregular rows on entire extension of undersurface of vein. Shape and proportions of some leg segments as in figure 64F–H. Fore basitarsus 14.8 times and hind basitarsus 6.8 times as long as wide. Calcipala almost reaching apex of second tarsomere (fig. 64K). Genitalia without special characters.

Pupa. Cocoon approximately slipper shaped, covering most of body but leaving gills exposed. Fabric of cocoon consisting of tightly woven fine threads, not forming open meshwork, and no apertures apparent. Cocoon light brown, length 4.5 mm. One (of two) specimens with cocoon encrusted with small foreign particles, the other one fully exposed. Total length of pupal body 5.0 mm; cephalopterothecal length 2.5 mm. Gills very similar to those of *G. flabellus,* maximum length 2.5 mm, color blackish; basal stalk shorter than wide (fig. 64N, Q, U), almost indiscernible. Primary branches short, indistinct in some cases, secondary filiform branches arising very close to base of gill. Shape of frontoclypeus as in *flabellus.* Platelets heavily verrucose, very numerous, their distribution as on thorax (see fig. 64I–L). Facial trichomes stout, spinelike (fig. 64M). Dorsocentral trichomes consisting of two stout spinelike setae and one longer and more slender seta (fig. 64S); dorsolateral trichomes very delicate, hairlike. Setae of abdominal tergite I stout (fig. 64S), length 32–45 μm; setae of tergite II short, spinelike (fig. 64T), length not more than 28 μm. Tergites III and IV each with 4 + 4 short, relatively slender

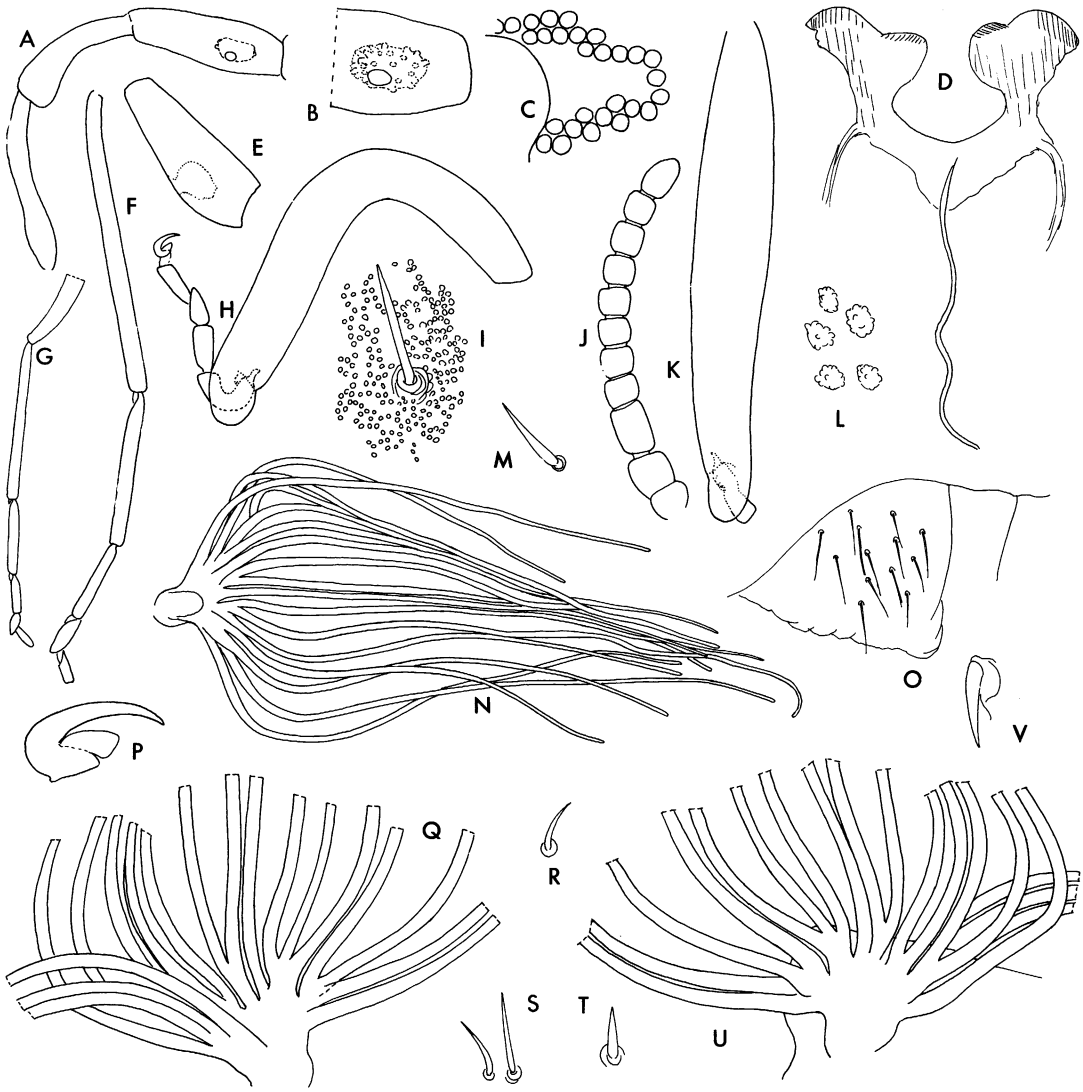

Fig. 64. *Gigantodax awa.* **A.** Maxillary palp of female. **B.** Sensory vesicle of maxillary palp of female. **C.** Fronto-ocular triangle. **D.** Genital fork. **E.** Second segment of maxillary palp of male. **F.** Foreleg of male. **G.** Portion of foreleg of female. **H.** Posterior tarsus, female. **I.** Trichome of thorax of pupa. **J.** Antenna of female. **K.** Posterior basitarsus of male, with second tarsal segment. **L.** Platelets of thorax of pupa. **M.** Facial trichome of frontoclypeus of pupa. **N.** Gill of female pupa. **O.** Gonapophyses of female. **P.** Claw of female. **Q.** Base of gill of female pupa, inner surface. **R.** Anterolateral trichome of thorax of female pupa. **S.** Setae of first abdominal tergite of female pupa. **T.** Spinelike seta of second abdominal tergite of female pupa. **U.** Base of gill of female pupa, outer surface, thorax of pupa. **V.** Hook on tergite IV.

hooks; anterodorsal setae (fig. 64R) slender, shorter than hooks. Setae of tergites VI–VIII slender, short, inconspicuous, length on tergite VII 32–35 μm. Spine-combs on tergites VI–VIII continuous, consisting on tergite VII of 39 spines, length 30–32 μm, viz., about as long as setae of this segment. Specialized setae of segments VIII and IX variously curved or twisted, but no branched setae observed. Sternite IV with short hooklike setae, one

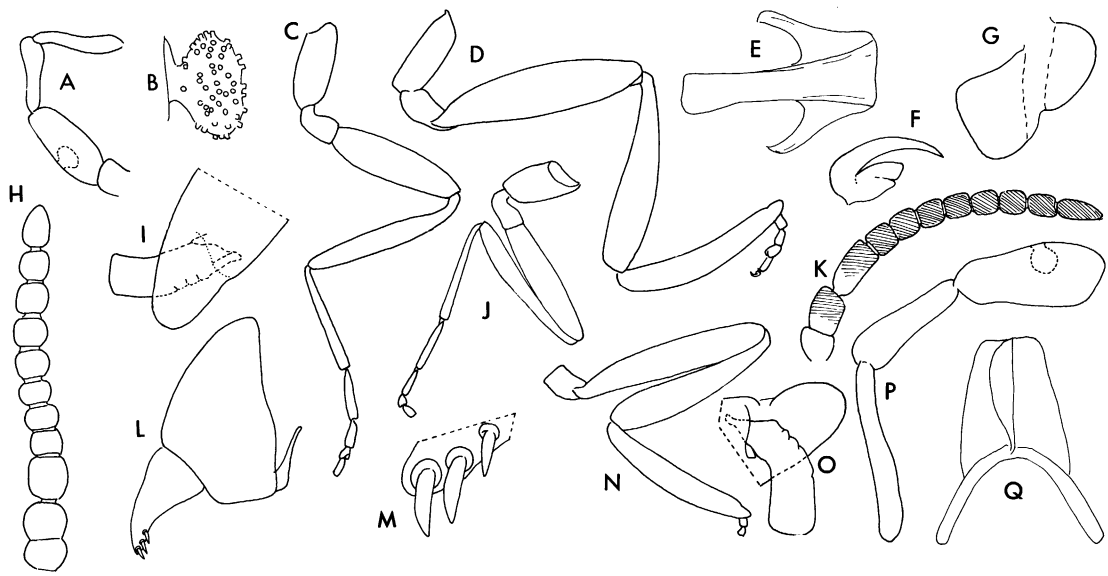

Fig. 65. *Gigantodax paramorum.* A–D, F–I. Female. **A.** Maxillary palp. **B.** Sensory vesicle. **C.** Foreleg. **D.** Hind leg. **E.** Median sclerite. **F.** Claw. **G.** Cercus and paraproct. **H.** Antenna. **I.** Calcipala, with second tarsal segment. J–Q. Male. **J.** Foreleg. **K.** Antenna. **L.** Basimere and distimere. **M.** Apical spines of distimere. **N.** Hind leg. **O.** Calcipala, with second tarsal segment. **P.** Maxillary palp. **Q.** Ventral plate.

central and 1 + 1 sublateral pair, as well as lateral single setae. Sternite V with 3 + 3, sternal plates VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Larva. Unknown.

HOLOTYPE: PERU: *Cuzco:* Machupicchu, 2070 m, April 18, 1971 (S. Coscarón; MLP), male (reared, and with associated pupal exuvia).

ALLOTYPE: Same data as holotype, one pharate female (with associated pupal exuvia).

ETYMOLOGY: Name taken from the Quechua *awa,* a twin, in reference to the great similarity of this species to another species of the genus, *G. flabellus.*

DISCUSSION: *Gigantodax awa* closely resembles *G. flabellus* from Ecuador. The differences found are as follows (with characters of *flabellus* given in parentheses):

Second segment of maxillary palp of female subcylindrical, ratio length/width 1:0.33 (elongate oval, ratio length/width 1:0.42); sensory vesicle small, palpal ratio 1:0.27 (sensory vesicle larger, palpal ratio 1:0.36); male with palpal ratio 1:0.36 small sensory vesicles (sensory vesicle larger, palpal ratio 1:0.23–0.25). Pupa with gill stalk extremely short, much wider than long (stalk 1.5 times as long as wide); pupa with platelets of frontoclypeus and thorax heavily verrucose (platelets from smooth to very faintly verrucose); setae of first abdominal tergite of pupa 32–45 mm long (50–70 μm long); anterodorsal setae of tergites III and IV of pupa slender (very stout).

According to pupal gill shape, *G. awa* and *G. flabellus* are closer to the Patagonian species than to those from Venezuela, Colombia, Ecuador, and Peru.

Gigantodax paramorum, new species

Figures 65A–Q, 66A–K, 67A–I

DIAGNOSIS: This species is distinguished from all others of the genus by the pupal gill branches originating from four strongly divergent primary branches.

DESCRIPTION: *Female.* Length of wings about 4 mm. Head blackish; clypeus from reddish brown to piceous. Antenna and maxillary palp dark brown; scapus and pedicellus orange. Scutum orange colored in specimens preserved in alcohol, dark reddish brown in

Fig. 66. *G. paramorum.* Pupa. **A.** Anterior portion of thorax with gills, dorsal view. **B–D.** Gills, different specimens. **E.** Frontoclypeus, female. **F.** Hook of tergite IV. **G.** Detail of thorax, trichome with platelets. **H.** Portion of thorax, with trichomes. **I.** Frontoclypeus of male pupa, with trichomes. **J.** Anterosublateral trichome tergite III. **K.** Chaetotaxy of tergites I and II.

dried specimens (from alcohol). Scutellum yellowish, metanotum as scutum. Pleural region light brown. Thoracic setae golden colored. Wing translucent, veins light brown. Setae on stem vein and on other veins dark. Halter whitish, capitulum slightly darkened. Legs pale yellow, bases and apices of femora and tibiae darkened; setae concolorous. Hairs of abdomen from brass to golden colored. Abdominal terga dark brown or piceous, with hind margin narrowly whitish.

Frontal angle 50°. Fronto-ocular triangle

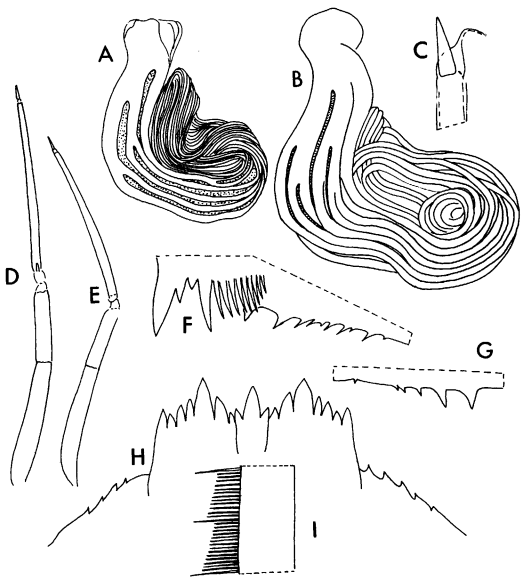

Fig. 67. *G. paramorum.* Larva. **A, B.** Histoblasts. **C.** Terminal sensillum of antenna. **D, E.** Antenna. **F.** Distal portion of mandible. **G.** Mandibular serrations. **H.** Anterior portion of hypostomium. **I.** Teeth of ray of cephalic fan.

about as high as wide. Shape and proportions of antennal segments as in figure 65H. Mandible with 25 or 26 teeth. Maxilla with about 35 teeth. Terminal segment of maxillary palp (fig. 65A) only slightly longer than penultimate. Second segment of maxillary palp elongate, suboval, ratio length/width = 1:0.45–0.48. Sensory vesicle small, oval, with short but distinct neck (fig. 65B); Sc with approximately 25 setae in two or three irregular rows; spinules present, in one or two rows, beginning slightly basal to level of insertion of Sc on C. R_s on apical portion dorsally with setae in one row, entire undersurface with setae in two irregular rows. A_1 not reaching wing margin. Shape and proportion of leg segments as in figure 65C, D; hind basitarsus 6.6 times as long as wide. Calcipala extending beyond middle of second tarsomere, falling considerably short of apex (fig. 65O). Basal tooth of claws as shown in figure 65F. Abdominal sterna with delicate setae only. Genitalia without special characters; cercus and paraproct as illustrated (fig. 65G).

Male. Length of wing 3.8 mm. Clypeus and maxillary palp brownish; setae of postocciput from golden colored to brown. Antenna brown, with scapus, base of pedicellus and base of first flagellomere orange colored. Scutum dark reddish orange, scutellum pale brown, metanotum similar to scutum. Pleuron light brown. Hairs of thorax golden colored, setae of posterior portion of scutum and on scutellum dark brown. Wings translucent; veins light brown. Setae on stem vein and on remaining veins dark. Halter light brown. Legs yellowish brown, tarsi somewhat darkened; hairs concolorous. Abdominal fringe and remaining short abdominal hairs brass colored. Abdominal tergites dark brown, center of disc of tergites slightly lighter; hind margin narrowly ivory colored.

Holoptic. Shape and proportions of antennal segments as in figure 65K; ratio length/width of first flagellomere 1:0.69. Terminal segment of maxillary palp 1.5 times as long as penultimate (fig. 65P). Sensory vesicle small, subglobular, with distinct neck. R_1 with setae in one row; spinules present, beginning somewhat basal to level of insertion of Sc on C, as or more numerous than setae. R_s with setae in one row on apical portion of upper surface, in from one to three rows on undersurface of veins. A_1 ending at considerable distance from wing margin. Shape and proportions of leg segments as in figure 65J, N. Fore basitarsus 13 times, hind tarsus 5.9 times as long as wide. Calcipala considerably surpassing apex of second tarsomere (fig. 65I). Distimere about as long as basimere (fig. 65L), wide at base with two large and one small apical spines (fig. 65M). Main body of ventral plate distinctly longer than wide (fig. 65Q). Median sclerite as shown in figure 65E.

Pupa. Cocoon of irregular shape, baglike, covering entire body of pupa including base of gills. Color of cocoon very light brown, formed of loose mesh, with many small "windows." Length of cocoon about 4.0 mm. Total length of body of pupa 3.5 mm; cephalopterothecal length 2.2 mm. Gills light brown, with filamentous branches on four strongly divergent primary branches (dorsal, dorsolateral, ventrolateral, and ventral) (fig. 66A–D). Extreme base of branches oblique and almost perpendicular to longitudinal axis of body of pupa, remainder of branches directed forward. Dorsal primary branch with four secondary branches, the first directed. Dorsal primary branch with four secondary branch-

es, the first one based far from primary branch, the second to fourth branches arising contiguously (trifurcate branching) or subcontiguously. Dorsolateral primary branch divided at short distance from base into two secondary branches, each of the latter bifurcates again so as to form a total of four terminal branches. Ventrolateral primary branch divided very close to its base, the dorsal arm bifid at a short distance from its base, the ventral arm with four terminal branches, one (the 14th) arising close to base of primary branch, the other three arising contiguously or subcontiguously. Ventral primary branch with one secondary branch arising at a short distance from base, further apicad with three terminal branches arising contiguously or subcontiguously. All branches very slender and elongate, the ventral longer than dorsal branches; apex of branches filiform. Surface of branches minutely dotted, distribution of dots as in *G. basinflatus*. Shape and proportion of frontoclypeus of female and male pupa shown in figure 66E–I; with numerous smooth or very slightly verrucose platelets. Facial trichomes in shape of slender spiniform setae. Thorax with numerous smooth platelets, irregularly arranged as shown in figure 66G. Three spinelike dorsocentral and two delicate, hairlike, dorsolateral trichomes. Setae of abdominal tergite I slender, comparatively long, 50–60 μm; setae of tergite II thicker and longer (fig. 66K), 60–70 μm. Tergites III and IV each with 4 + 4 slightly elongate hooks (fig. 66F); anterosublateral setae slender, about as long as hooks (fig. 66J). Setae of tergites V–VIII with small interruptions, consisting on tergite VII of about 18 spines, length 25–30 μm, viz., half as long as setae of this tergite. Specialized setae of segments VIII and IX simple, from almost straight to slightly curved, not branched. Sternite IV with very small setae; V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 7 mm; width of head capsule 0.7 mm. Body shape as usual for the genus; ventral papillae distinct. Body color whitish, with faint purple hypodermal pigment. Head light brown; spots of cephalic apotome distinct. Gular region not distinctly darker than rest of head, with faint median longitudinal band white. Antenna about as long as stem of cephalic fan, distinctly pigmented, third segment darkest. Shape of antenna as in figure 67D, E; ratio of segments I–III = 1:0.5–0.6:1.2–1.4. Terminal sensillum about 3.5 times as long as wide at base; in some specimens accompanied by long membranous projection (fig. 67C). Cephalic fan with 22–28 large rays, their small teeth distinctly shorter than long ones (fig. 67I). Mandible (fig. 67F, G) with 8–10 inner teeth and 6–10 marginal serrations. Maxillary palp about 2.5 times as long as wide. Hypostomium with median tooth short of level of corner tooth apex, but past level of third intermediate tooth apex (fig. 67H). Lines connecting apices of fourth lateral tooth and corner tooth meeting at angle of about 110°. Hypostomium with 5–8 lateral serrations and 5–7 hypostomial teeth. Cervical sclerites as in *cormonsi*. Histoblast as in figure 67A, B; characterized by the comparatively long primary branches. Perianal scales large and numerous, forming a complete circumanal ring. Recurrent struts normal. Crochet ring with about 100 rows of about 21 hooks each.

HOLOTYPE: COLOMBIA: *Cundinamarca:* "Buenos Aires," near La Siberia, W of La Calera, 3050 m, July 15, 1967 (P. and B. Wygodzinsky; AMNH), male (reared, and with associated pupal exuviae).

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, one pupa. COLOMBIA: *Cundinamarca:* road from Sibate to Aguadita, just below San Miguel, 2800 m, July 5, 1967 (P. and B. Wygodzinsky; AMNH), one female, allotype, one female, paratype (both reared, and with associated pupal exuviae) larvae; road from Usme to Paramo de Chisaca (or Sumapaz), 3300 m, July 11, 1967 (P. and B. Wygodzinsky; AMNH), three males, paratypes (reared, and with their associated pupal exuviae); Paramo de Guasca, 3300 m, July 20, 1967 (P. and B. Wygodzinsky; AMNH), pupae.

ETYMOLOGY: This species is named for its occurrence on the paramos.

BIOLOGY: This is a rare species, at least in July when other species of *Gigantodax* are abundant. The few pupae obtained were found in fast-flowing streams not over 1 ft wide, located in open paramo grassland, with a water temperature between 9 and 17°C. The

water was clear, but there was considerable organic deposit on bottoms of streams and on blades of grass on which the pupae of this and of other species of *Gigantodax* were collected.

DISCUSSION: This species is superficially very similar to *G. destitutus,* at least in the male and the pupa; the female and larva are not known. However, *G. paramorum* differs from *destitutus* by numerous characters, which may indicate that there is no very close relationship between the two. The male of *paramorum* is distinguished by the annulate basal portion of the antennae and, in the genitalia, by the comparatively narrow ventral plate. The pupa of *paramorum* differs from that of *destitutus* by having shorter primary gill branches, such as in the 12th and 16th branches. The facial and dorsocentral trichomes of *paramorum* are spinelike, not hairlike as in *destitutus,* and the number of hooks on abdominal sternite V is the normal 3 + 3, not 2 + 2 as in *destitutus.* The spinelike facial trichomes is a synapomorphic character shared with *flabellus* and *awa.*

Gigantodax viannamartinsi Ramirez Perez

Gigantodax viannamartinsi Ramirez Perez, 1980: 56, ill.; 1983: 73.

DISCUSSION: *Gigantodax viannamartinsi* was described from a male and pupa from Merida, Venezuela, and is very close to *G. paramorum.* Both have in common the wing size, coloration, and proportion of the calcipala in the male. The shape of the pupal gill branches is also similar, but the illustrations of *viannamartinsi* show different arrangements and the frontoclypeus and thorax platelets are not smooth. As we were unable to examine specimens used by Ramirez Perez for his description, and because he did not describe females and larvae, we prefer to maintain them as a separate species.

Gigantodax ortizi, Wygodzinsky

Figures 68A–N, 69A–J, 70A–L, 71A–F, 72A–S

Gigantodax ortizi Wygodzinsky, 1973: 246. Vulcano, 1981: 276. Ramirez Perez, 1983: 73.

DIAGNOSIS: Distinguished by dark purple females and dark brown males with very long calcipala that reach near the apex of the second tarsomere, gill branches forming a tight bundle, and abundant platelets on frontoclypeus and thorax of pupae.

REDESCRIPTION: *Female.* Length of wings 3.7–3.9 mm. Antenna and maxillary palp grayish brown; scapus and pedicellus orange brown, contrasting with dark flagellum. Scutum dark purple, scutellum light brown; metanotum as in scutum. Pleura light brown, with purple pruinescence. Thoracic setae golden yellow. Wing translucent; veins light brown. Setae on stem vein very dark; the remaining wing setae also dark. Halter very light brown. Legs light brown, their hairs concolorous. Abdominal fringe and remaining abdominal hairs brass colored. Abdominal tergites piceous, hind margin narrowly ivory colored; center of disc of tergites faintly lightened.

Frontal angle about 45°. Fronto-ocular triangle (fig. 68F) distinctly higher than wide. Shape and proportions of antennal segments as in figure 68C. Mandible with teeth on inner margin only, numbering 22–25 (fig. 68B). Maxilla with 36–38 teeth. Distal segment of maxillary palp 1.5 times as long as penultimate (fig. 68D). Second segment of maxillary palp subelliptical, with sides almost parallel; ratio length/width = 1:0.42–0.44. Sensory vesicle subglobular (fig. 68E); Sc with 25–28 hairs. Setae on R in two or three irregular rows, on R_1 in one row, interspersed with numerous spinules, the latter beginning slightly basal to level of insertion of Sc on C, arranged in one or two rows; spinules more numerous than hairs. R_1 with setae in one row on apical portion of dorsal surface, two or three irregular rows on entire extension of undersurface of vein (fig. 68A). A_1 almost reaching wing margin. Shape and proportions of some leg segments as illustrated (fig. 68I, J). Hind basitarsus approximately 7.5 times as long as wide. Calcipala almost reaching apex of second tarsomere (fig. 68N). Basal tooth of claws large, as in figure 68L. Abdominal sterna with only delicate hairs. Eighth sternite and gonapophyses as in figure 68K. Paraproct with small process (fig. 68H); cercus very low. Genital fork as in figure 68G; spermatheca subglobular, neck of spermathecal duct membranous; spicules as in figure 68M.

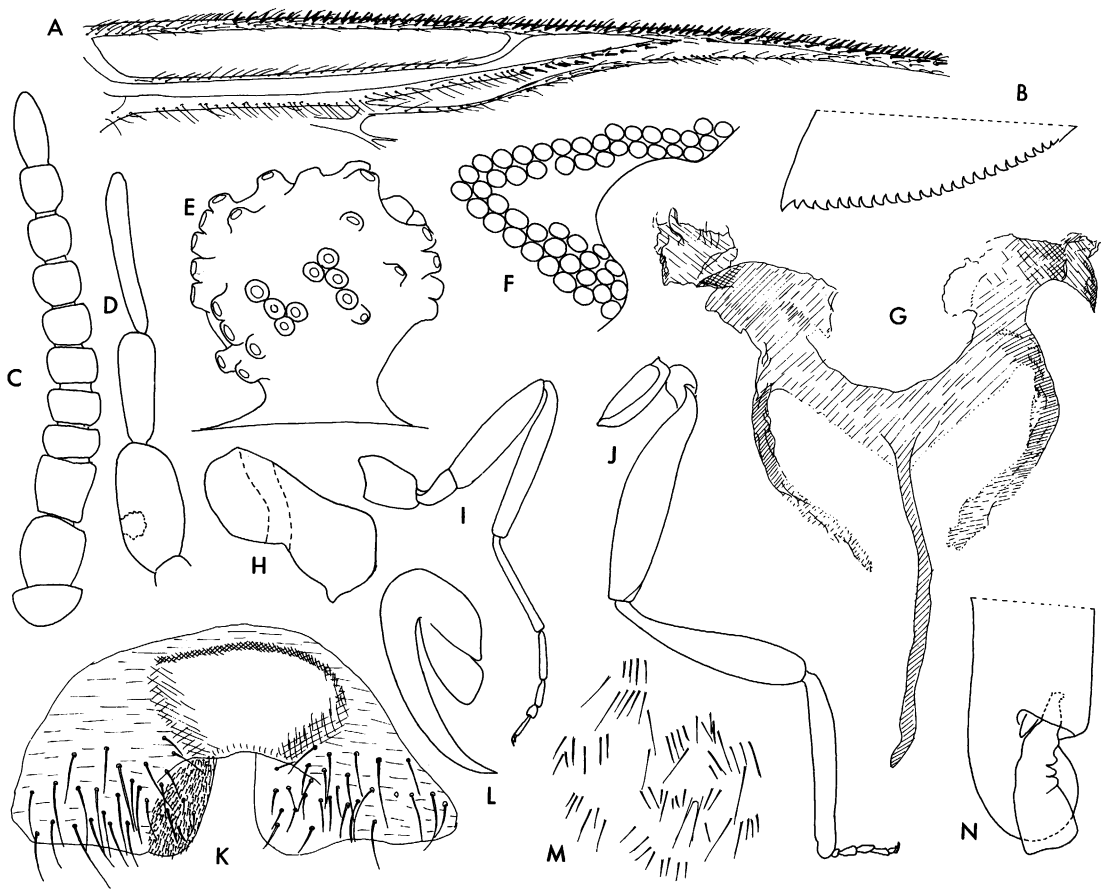

Fig. 68. *Gigantodax ortizi.* Female. **A.** Anterior portion of wing. **B.** Apex of mandible. **C.** Antenna. **D.** Maxillary palp. **E.** Sensory vesicle of maxillary palp. **F.** Fronto-ocular triangle. **G.** Genital fork. **H.** Cercus and paraproct. **I.** Foreleg. **J.** Hind leg. **K.** Eighth sternite with gonapophyses. **L.** Claw. **M.** Microstructure of inside of spermatheca. **N.** Calcipala with second tarsal article.

Male. Length of wing 3.2–3.6 mm. Color as in female, but scutum dark chestnut brown.

Holoptic. Shape and proportions of antennal segments as in figure 69A; ratio length/width of first flagellomere 1:0.48–0.67. Terminal segment of maxillary palp 1.5 times as long as penultimate (fig. 69B). Sensory vesicle small, globular, with short neck (fig. 69C). Wing as in female, but Sc with about 20 hairs. Shape and proportions of some leg segments as in figure 69D, E. Fore basitarsus 10.4–12 μm, 12.2 times as long as wide; hind basitarsus 5.9–6.2 times as long as wide. Calcipala (fig. 69F) almost reaching apex of second tarsomere. Distimere over two-thirds as long as basimere and with two apical spines. Main body of ventral plate about as long as wide (fig. 69H, I). Ventral plate with median sclerite and endoparameral organ as in figure 69G–J.

Pupa. Cocoon, when well preserved, covering entire body except gills; in most specimens leaving anterior declivity of thorax with head exposed (fig. 70A, B). Fabric of cocoon dark brown consisting of very coarse, irregular mesh with wide apertures. In most specimens cocoon incrusted with large amounts of easily detached organic material so as to completely obscure threads. Length 4.0–5.2 mm. Total length of body of pupa 3.5–4.0 mm, cephalopterothecal length 2.2 mm. Gill light brown, with forwardly directed filiform branches, forming a tight bundle or only slightly diverging from each other. Basal stalk

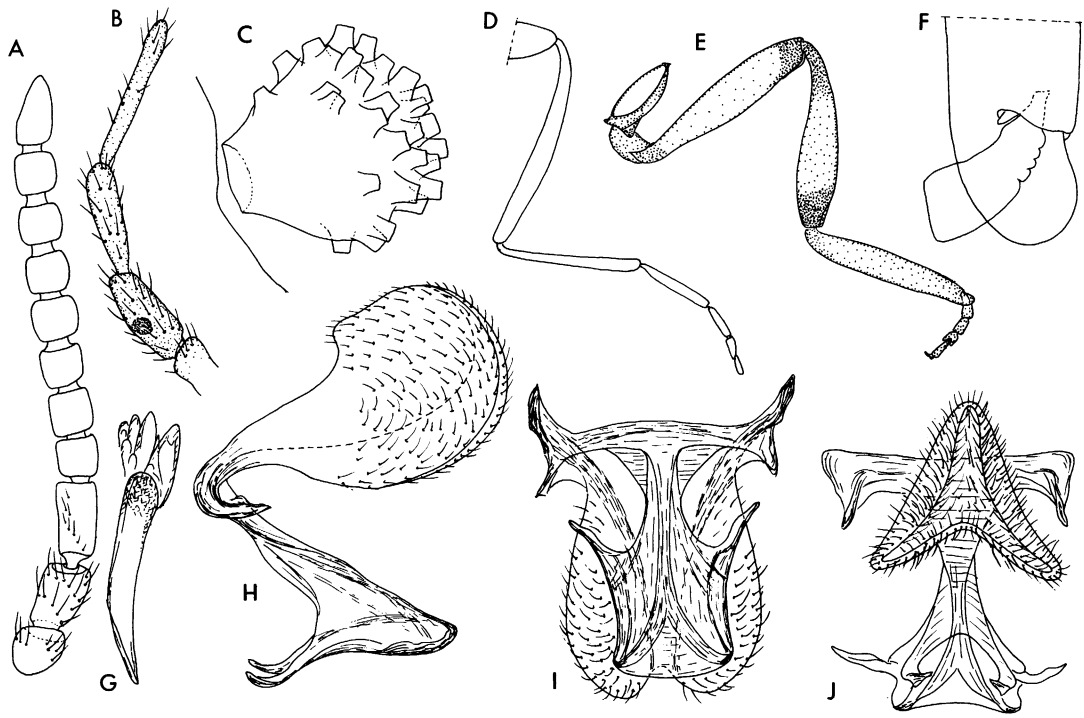

Fig. 69. *G. ortizi.* Male. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle of maxillary palp. **D.** Portion of foreleg. **E.** Hind leg. **F.** Calcipala, with second tarsal article. **G.** Endoparameral organ. **H–J.** Ventral plate with median sclerite in different views.

of gills from two to three times as long as wide in narrow portions (fig. 70A, B, D–G, I). Primary branches numbering five or six, only very slightly diverging from direction of longitudinal axis of basal stalk. Terminal branches in most cases branching off dichotomously at different levels, some at considerable distance from base of gill. Total length of intact gill up to 3.5 mm. Surface of branches with more or less spirally arranged minute dots of roughly two sizes (fig. 70C). Apex of gill branches rounded. Outline shape of frontoclypeus of male and female as in figures 70H, 71B–D; platelets not very numerous, arranged in small groups (fig. 71B); their surface smooth, but under certain illumination showing stellar optical pattern. Facial trichomes slender, spinelike. Thorax with platelets arranged in small, in many instances rosette-shaped groups; distribution of platelets characterized by extensive bare spaces between groups and/or isolated platelets (fig. 71C, F). Dorsocentral trichomes consisting of two elongate, spinelike setae and one seta varying from spine to hairlike. Dorsolateral trichomes delicately hairlike. Setae of abdominal tergite I (fig. 71E) long and slender, their length 70–80 μm; setae of abdominal segment II short, spinelike, their length 35–50 μm. Tergites III and IV each with 4 + 4 short hooks (fig. 70L). Anterodorsal setae (fig. 70K) stout, slightly shorter than hooks. Setae of tergites VI–VIII slender, their length on tergite VII 35–50 μm. Spine-combs on tergites VI–VIII continuous or with slight interruption, consisting on tergite VII of 25–32 spines, length 20–25 μm, viz., about half as long as the setae of this segment. Specialized setae of segments VIII and IX from straight to variously curved, only very rarely branched. Sternite V with 3 + 3, VI with 2 + 2 and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous (fig. 71A).

Mature larva. Length 6.0–7.0 mm; width of head capsule 0.6 mm. Body shape as usual

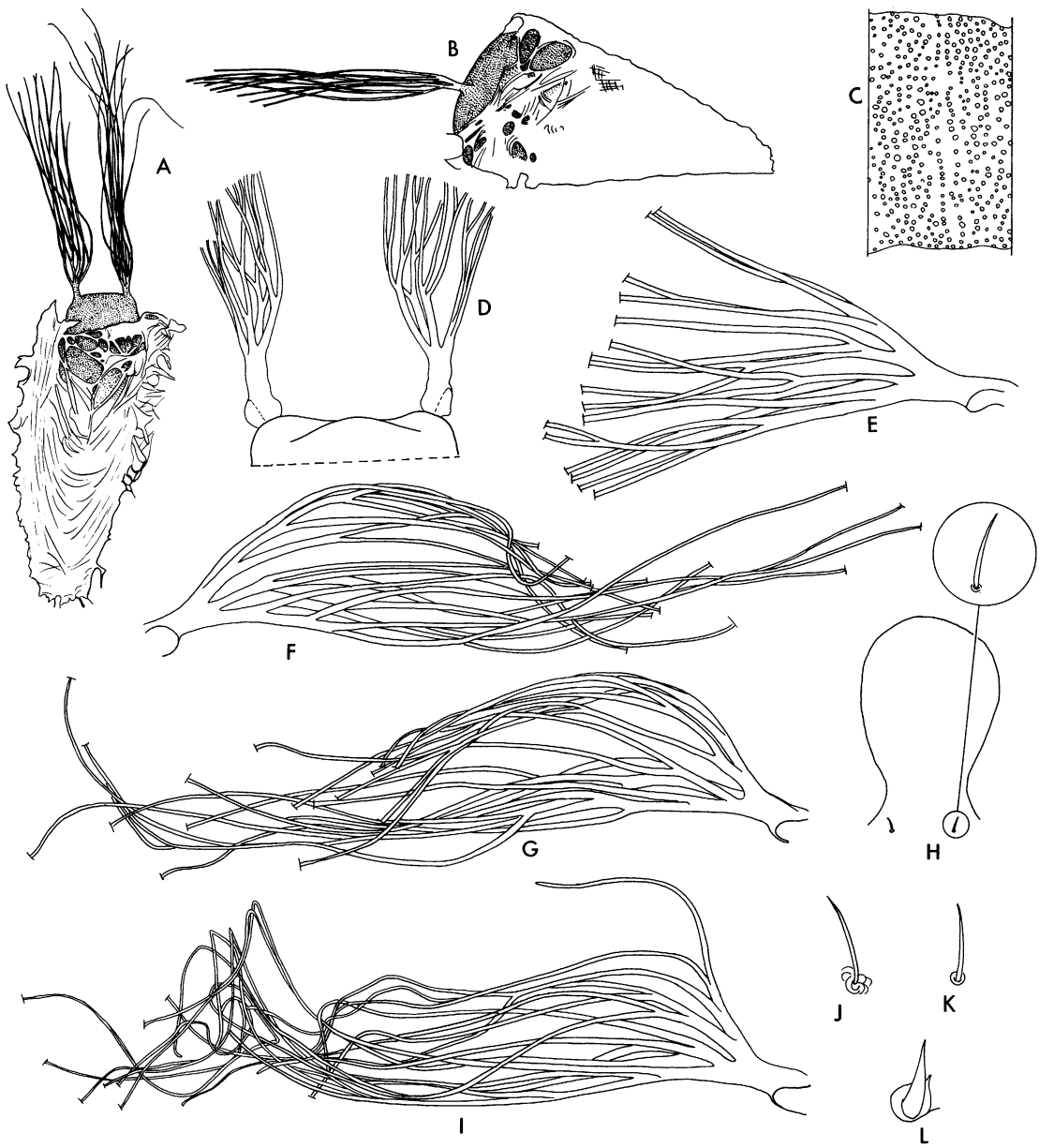

Fig. 70. *G. ortizi.* Pupa. **A.** Pupa in cocoon, dorsal view. **B.** Same, lateral aspect. **C.** Microstructure of gill branch. **D.** Anterior portion of body with base of gills, dorsal view. **E.** Basal part of gill, specimens from La Siberia. **F, G.** Gills, specimens from Sumapaz. **H.** Frontoclypeus of male. **I.** Gill, specimens from Sumapaz. **J.** Trichome from base of clypeus. **K.** Dorsolateral setae of tergite IV. **L.** Hook of tergite IV.

for genus; ventral papillae well developed (fig. 72E). Almost entire body of larva with distinct purple hypodermal pigment. Head light brown; spots of cephalic apotome faint, blending to background (fig. 72L). Hyposto-mial bridge not distinctly darker than rest of head, with faint median longitudinal line whitish. Antenna as long as or slightly longer

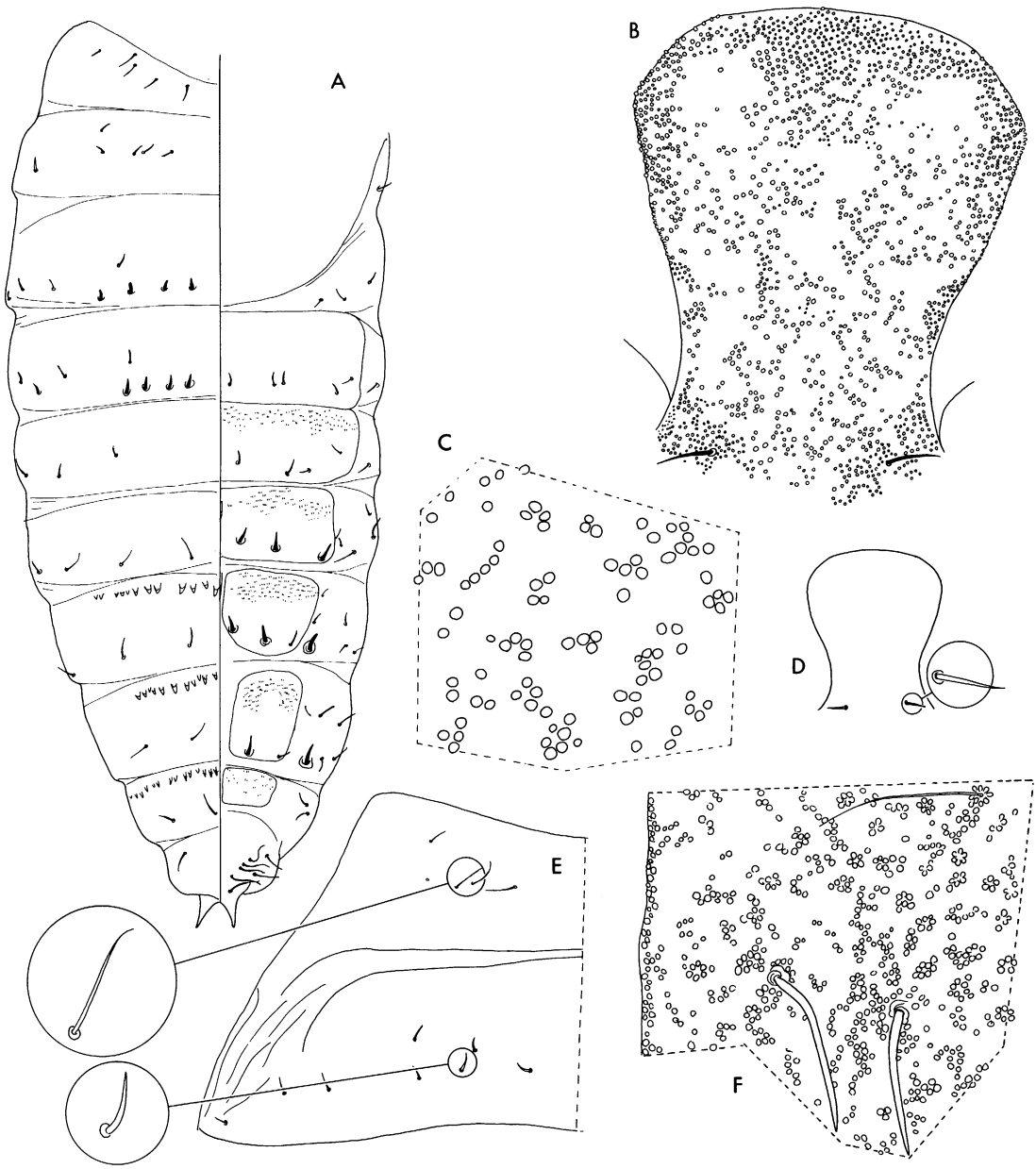

Fig. 71. *G. ortizi.* Pupa. **A.** Abdomen, dorsal view at left, ventral view at right. **B.** Frontoclypeus of female with platelets. **C.** Distribution of platelets on thorax. **D.** Outline of frontoclypeus of female. **E.** Chaetotaxy of I and II abdominal tergites. **F.** Portion of thorax, with trichomes.

than stem of cephalic fan, faintly pigmented, third segment darkest. Shape of antenna as in figure 72B, K; ratio of segments I–III = 1:0.48–0.58:1.09–1.39. Terminal sensillum about five times as long as wide, accompanied by elongate lamellar structure (fig. 72C). Cephalic fan with 22–26 large rays, their small teeth not much shorter than large teeth (fig. 72R). Mandible (fig. 72F, H–J, O) with eight to nine inner teeth and five to eight marginal serrations. Maxillary palpi slender, about 2.7 times as long as wide. Hypostomi-

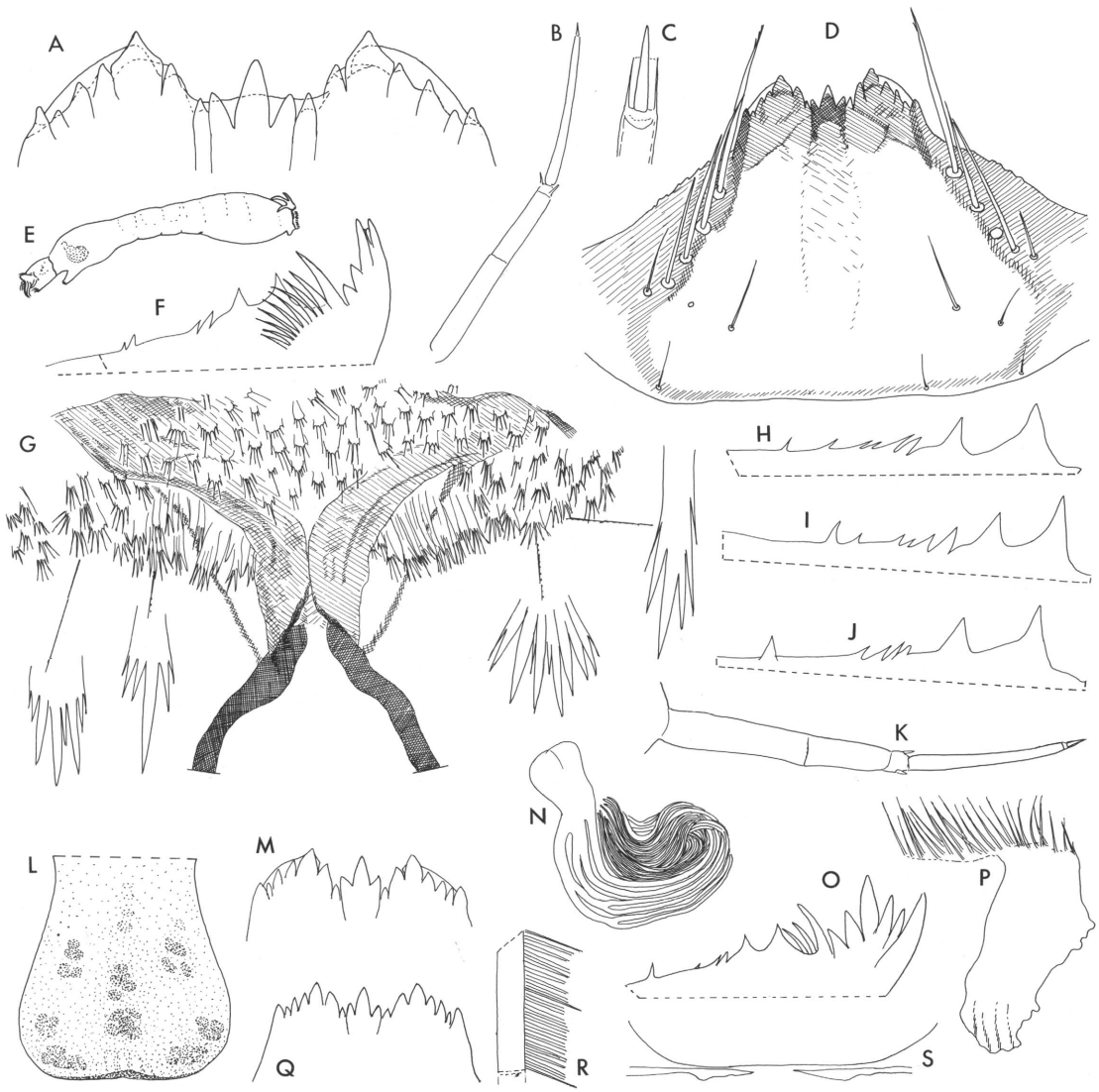

Fig. 72. *G. ortizi.* Larva. **A.** Anterior portion of hypostomium. **B.** Antenna. **C.** Terminal sensillum of antenna. **D.** Hypostomium. **E.** Larva, side view. **F.** Apical portion of mandible. **G.** Anal sclerite, annular portion not shown. **H–J.** Mandibular serrations. **K.** Antenna. **L.** Cephalic apotome. **M, Q.** Apical portion of hypostomium, different specimens. **N.** Gill histoblast. **O.** Apex of mandible. **P.** Lateral sclerite of proleg. **R.** Teeth of ray of cephalic fan. **S.** Cervical region.

um (figs. 72D, M, Q) with median tooth short of level of corner tooth apex, but distinctly past level of third intermediate tooth apex. Line connecting apices of fourth lateral tooth and corner tooth forming angle of 115–120°. Cervical sclerite as in figure 72S. Gill histoblast as in figure 72N, with bifurcations at considerable distance from stalk of gill. Color of mature gill histoblast brown, its base lighter. Proleg sclerite as in figure 72P. Perianal scales very well developed, extremely numerous, forming complete circumanal ring (fig. 72G). Crochet ring with 110–120 rows of 18–20 hooks each.

MATERIAL EXAMINED: VENEZUELA: *Merida:* road from Apartaderos to Santo Do-

mingo, 3400–3500 m, Feb. 16–28, 1968 (P. and B. Wygodzinsky; AMNH), 1 male holotype, 1 female allotype, 2 males, 4 female paratypes, pupae, and larvae. COLOMBIA: *Cundinamarca:* 5 km S of Usme, 3000 m, July 27, 1967 (P. and B. Wygodzinsky; AMNH), 4 males, 4 females (reared, and with associated pupal exuviae), pupae, and larvae; road from Usme to Paramo de Chisaca (or Sumapaz), 3200–3300 m, June 30, 1965, July 11, 1967, July 27, 1967, Aug. 28, 1969 (P. and B. Wygodzinsky; AMNH), 6 males, 12 females (all reared, and with associated pupal exuviae, pupae, and larvae); Paramo de Chisaca (Sumapaz), 3500 m, June 30, 1965 (P. and B. Wygodzinsky; AMNH), 1 male, 2 females (reared, and with associated pupal exuviae); road from Bogota to Choachi, 3100 m, July 12, 1967 (P. and B. Wygodzinsky; AMNH), 2 larvae; Buenos Aires, near La Siberia, E of La Calera, 3050 m, July 17, 1967, Aug. 26, 1969 (P. and B. Wygodzinsky; AMNH), 8 females (all reared, and with associated pupal exuviae); Paramo de Guasca, 3100 m, July 20, 1967 (P. and B. Wygodzinsky, E. W. Schmidt-Mumm; AMNH), 1 female (reared, and with associated pupal exuvia), larvae. *Distrito Especial:* Rio San Francisco, E of Bogota, 2750 m, July 17, 1967 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal exuvia), pupae. *Boyaca:* Paramo de Tota, W slope, 3300 m, July 8, 1967 (P. and B. Wygodzinsky, E. W. Schmidt-Mumm; AMNH), 1 pupa, larvae.

BIOLOGY: Most specimens were collected in small, shallow, fast flowing streams or irrigation ditches, from 15–30 cm wide and not more than 10 cm deep. These watercourses, situated generally in pastures and receiving no or very little shade, had temperatures between 11 and 16°C. Most carried considerable amounts of organic detritus covering the vegetation to which the pupae were attached as well as the pupae themselves. All larvae and pupae were attached to trailing grass blades, in very large numbers in some cases. Generally pupae were located on the undersides of grass blades along the midrib. No larvae or pupae were found on the undersides of stones. In the conditions above, specimens of *ortizi* (and of the related *multituberculatus* with which it was frequently associated) were generally more numerous than any other species of *Gigantodax.* We hypothesize that this is due to the greater tolerance that *ortizi* and *multituberculatus* have to eutrophic streams.

DISCUSSION: *Gigantodax ortizi* belongs to a group of species characterized in the pupal stage by the possession of a gill with 18 filamentous branches arranged in a rather tight, forwardly extending bundle, with a proportionately elongated basal trunk; the other species are *multituberculatus, laevigatus, patihuaycensis,* and *zumbahuae.* Unique characters of *Gigantodax ortizi* are the dark purple color of the female scutum, the unusually high number (36–38) of maxillary teeth, the unusually small palpal sensory vesicle in females, large cocoon apertures, and by the numerous smooth platelets on the pupal thorax, which are arranged in groups and often distinctly separated from other such glabrous areas.

Gigantodax multituberculatus, new species

Figures 73A–T, 74A–U

DIAGNOSIS: *G. multituberculatus* is close to *G. ortizi,* from which it especially differs by the light color in the imagos, the cocoon covering all of the body, and very abundant platelets on the head and thorax.

DESCRIPTION: *Female.* Length of wing 3.9–4.2 mm. Head black; pilosity brass or silver colored. Antenna and maxillary palp piceous; scapus and pedicellus dark orange. Scutum pale reddish brown; scutellum and metanotum of approximately the same color. Pleura yellowish brown, somewhat darker on upper portion. Thoracic setae from brass colored to yellowish. Wing translucent; veins light brown. Setae of stem vein and other veins dark. Halter yellowish white. Legs light brown; hairs concolorous. Abdomen dull piceous; hind margin of tergites narrowly white in some specimens. Abdominal fringe from brass to golden colored.

Frontal angle about 45°. Fronto-ocular triangle distinctly higher than wide. Shape and proportions of antennal segments as in figure 73K. Mandible with 25–28 teeth. Terminal segment of maxillary palp about 1½ times the length of penultimate (fig. 73B). Second segment of maxillary palp elongate oval (fig.

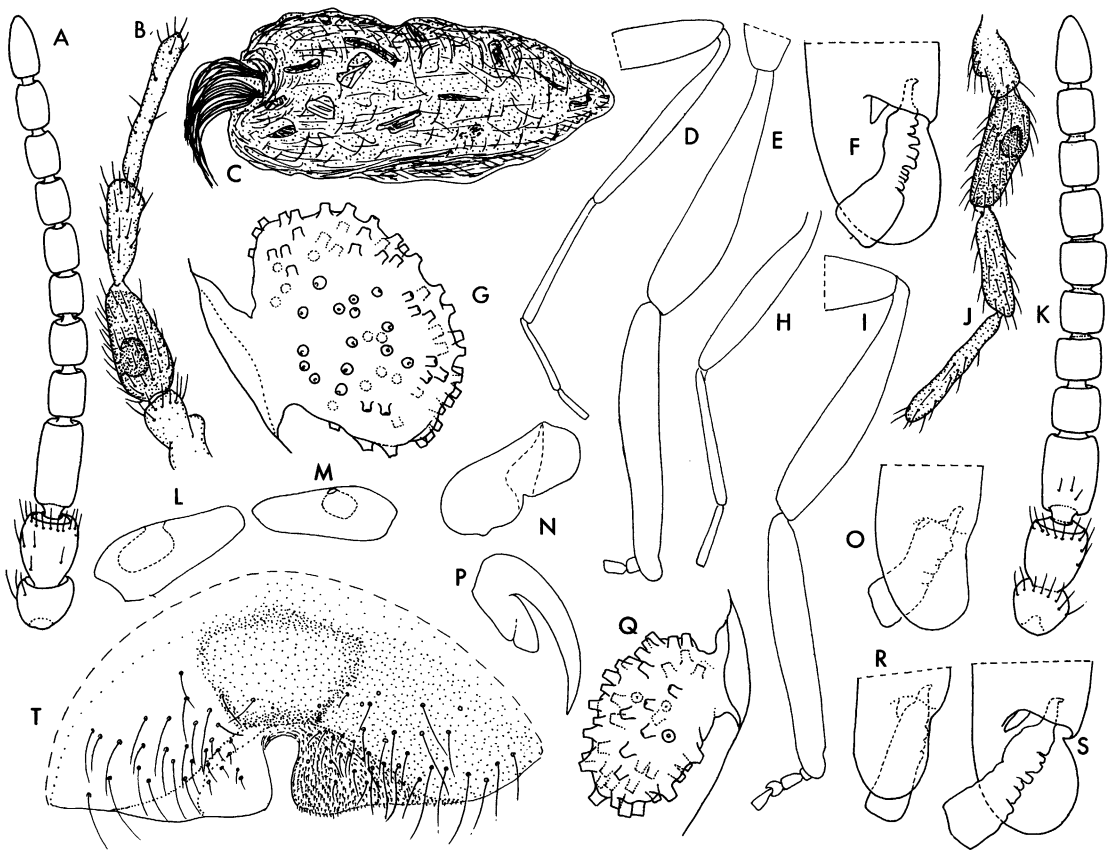

Fig. 73. *Gigantodax multituberculatus.* **A.** Antenna of male. **B.** Maxillary palp of female. **C.** Pupa in cocoon, side view. **D.** Foreleg of male. **E.** Hind leg of male. **F.** Calcipala of female, with second tarsal segment. **G.** Sensory vesicle of maxillary palp of female. **H.** Portion of foreleg of female. **I.** Hind leg of female. **J.** Maxillary palp of male. **K.** Antenna of female. **L.** Second article of maxillary palp, female. **M.** Same, male. **N.** Cercus and paraproct. **O.** Calcipala of female with second tarsal segment. **P.** Claw of female. **Q.** Sensory vesicle of maxillary palp. **R, S.** Calcipala of male, with second tarsal segment. **T.** Eighth sternite and gonapophyses.

73B, L); ratio length/width = 1:0.44–0.48. Sensory vesicle much longer than wide (fig. 73G). Chaetotoxy of wing veins as in *G. ortizi.* Shape and proportions of leg segments as in figure 73H, I. Hind basitarsus 6.58–6.97 times as long as wide. Calcipala almost reaching apex of second tarsomere (fig. 73F, O). Basal tooth of claw subrhomboidal (fig. 73P). Eighth abdominal sternite with only delicate hairs (fig. 73T). Cercus and paraproct as in figure 73N. Genital fork and spermatheca as in *ortizi.*

Male. Length of wing 3.7–3.9 mm. Color much as in female, but scutum bright reddish orange, and pleura in some cases yellowish. Abdominal tergites velvety piceous or black, with hind borders very narrowly margined with white.

Holoptic. Shape and proportions of antennal segments as in figure 73A; ratio length/width of first flagellomere 1:0.5. Terminal segment of maxillary palp slightly longer than penultimate (fig. 73J). Sensory vesicle subelliptical, with short neck (figs. 73M, Q). Wing as in female, but Sc with only about 20 hairs. Shape and proportions of leg segments as in figures 73D, E. Fore basitarsus 14.7 times, hind basitarsus 7.1 times, as long as wide. Calcipala almost reaching apex of second tarsomere (fig. 73S). Genitalia as in *ortizi.*

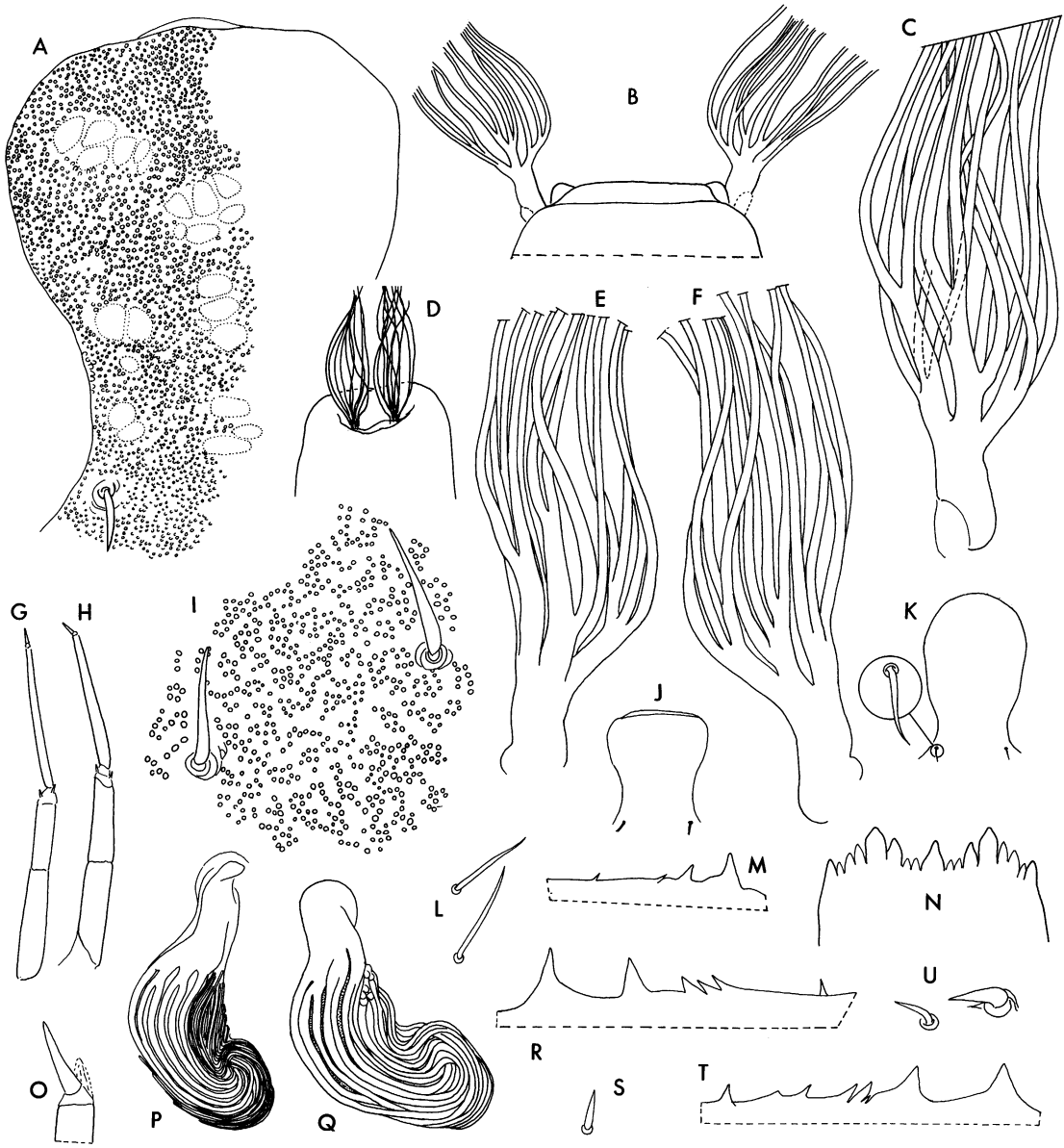

Fig. 74. *G. multituberculatus.* **A.** Frontoclypeus of female pupa. **B.** Head of pupa with insertion of gills, dorsal view. **C–F.** Gills. **G, H.** Antennae of larva. **I.** Portion of thorax of pupa, with platelets and trichomes. **J.** Frontoclypeus of female. **K.** Same, male. **L.** Setae of abdominal tergite I of pupa. **M.** Mandibular serrations. **N.** Anterior region of hypostomium. **O.** Terminal sensillum of antenna. **P, Q.** Gill histoblasts. **R.** Mandibular serrations. **S.** Seta of abdominal tergite II. **T.** Mandibular serrations. **U.** Seta and hook of tergite IV.

Pupa. Cocoon, when well preserved, covering entire body except gills (fig. 73D). Fabric of cocoon consisting of tightly woven fine threads, not forming open meshwork; color of cocoon light brown. In most specimens, cocoon covered with large amount of fine organic detritus, forming an oval bag covering entire cocoon and basal portion of gills; this material not easily detachable from substrate. Length of cocoon 4.0–4.5 mm. Total length

of pupal body 3.5–4.0 mm, cephalopterothecal length 2.3–2.4 mm. Gills light brown, arrangement very similar to those of *G. ortizi.* Basal stalk of gills about twice as long as wide (fig. 74B–F). Five or six primary branches, most diverging only slightly from direction of longitudinal axis of basal stalk, except dorsal, inner primary trunk the base of which is directed mesad. Terminal branches arising dichotomously at different levels, mostly close to base to primary branches. Total length of intact gills 3 mm. Shape and proportions of frontoclypeus of female and male as in figure 74J, K; platelets numerous, faintly verrucose, rather uniformly distributed (fig. 74A). Facial trichomes stout, spinelike. Thorax with platelets faintly verrucose, more or less uniformly distributed (fig. 74I), or, when forming groups, such groups in most cases connected. Dorsocentral trichomes consisting of two stout, spinelike setae and one seta varying from spine to hairlike; dorsolateral trichomes delicately hairlike. Setae of abdominal tergite I hairlike (fig. 74L), their length 50–60 μm; setae of tergite II stout, spinelike (fig. 74S), their length 21–31 μm. Tergites III and IV each with 4 + 4 short hooks (fig. 74U). Anterodorsal setae (fig. 74U) short and stout. Setae of tergites VI–VIII very weakly developed, length on tergite VII 20–25 μm. Spinecombs on tergites VI–VIII continuous or with very short interruptions, consisting on tergite VII of 29–39 spines, with length 25–30 μm, viz., as long as or longer than setae of this segment. Specialized setae of segments VIII and IX variously curved but not branched. Sternite IV with short, curved, spinelike setae, single or paired. Sternite V with 3 + 3, sternal plate VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length about 7.3 mm; width of head capsule about 0.7 mm. Body shape as usual for genus; ventral papillae well developed. Almost entire body of larva with purple hypodermal pigment, from faint to distinct. Head light brown; spots of cephalic apotome from distinct to blending into background. Hypostomial bridge not distinctly darker than rest of head. Antenna as long as or slightly longer than stem of cephalic fan, faintly pigmented, third segment darkest. Shape of antenna as in figure 74G, H; ratio of segments I–III = 1:0.68–0.73:1.24. Terminal sensillum about four times as long as wide at base, accompanied by short lamellar structure (fig. 74O). Cephalic fan with about 23 large rays, their small teeth not much shorter than large teeth (as in *ortizi,* fig. 72R). Mandible (fig. 74M, R, T) with eight to nine inner teeth and six to seven marginal serrations. Maxillary palp about 2.5 times as long as wide. Hypostomium (fig. 74N) with median tooth falling short of level of corner tooth apex, but slightly past level of of third intermediate tooth apex. Line connecting fourth lateral tooth apex and corner tooth meeting at angle of about 105°. Cervical sclerite as in *ortizi.* Gill histoblast as in figure 74P, Q, characterized by bifurcations situated comparatively close to trunk of gill. Color of mature histoblast brown, its base lighter. Perianal scales well developed, forming complete circumanal ring. Crochet ring with 110–120 rows of 20–22 hooks each.

HOLOTYPE: COLOMBIA: *Cundinamarca:* Buenos Aires, near La Siberia, E of La Calera, 3050 m, July 17, 1967 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female, allotype, 9 males, and 5 females, paratypes (all reared, and with associated pupal exuviae), pupae and larvae; ibid., Aug. 26, 1969 (P. and B. Wygodzinsky; AMNH), 6 males, 6 females, paratypes (all reared, and with associated pupal exuviae), pupae; Paramo de Guasca, 2850 m, July 20, 1967 (P. and B. Wygodzinsky; AMNH), pupae; road from Zipaquira to Pacho, 3000–3050 m, July 22, 1967 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal exuvia), pupae and larvae; road from Bogota to Choachi, E slope, 2800 m, July 13, 1967 (P. and B. Wygodzinsky; AMNH), larvae; road from Sibate to Aguadita, 2270 m, July 5, 1967 (P. and B. Wygodzinsky; AMNH), 1 male (reared, and with associated pupal exuviae); 2 km SE Alban, 2400 m, Aug. 6, 1967 (P. and B. Wygodzinsky; AMNH), 2 males, 2 females (reared, and with associated pupal exuviae), pupae. *Distrito Especial:* Rio San Francisco, 2 km E of Bogota, 2750 m, July 17, 1967 (P. and B. Wygodzinsky; AMNH), pupae. *Boyaca:* near N shore of Lake Tota, 3050 m,

July 8, 1967 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal exuvia). *Cauca:* road from Popayan to Purace, 3300 m, Aug. 17, 1967 (P. and B. Wygodzinsky; AMNH), pupae, E of Silvia, 2900 m, Aug. 24, 1967 (P. and B. Wygodzinsky; AMNH), 1 pupa. ECUADOR: *Pichincha:* road from Quito to Papallacta, 3300 m, July 20–Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), 2 females (reared, and with associated pupal exuviae); Paramo de Guamani, 3600 m, Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal exuvia) pupae. *Chimborazo:* Yerba Buena, 2630 m, road from Rio Bamba to Santiago, Nov. 7, 1986 (S. Coscarón; MLP): one pupa and larvae.

ETYMOLOGY: The name of the species is taken from the Latin *multus,* much, and *tuberculum,* small swelling, in reference to the large number of platelets, or tubercles, on the frontoclypeus and thorax of the pupa.

BIOLOGY: The habitat preferences of the aquatic phases of this species are the same as those of *G. ortizi* with which it frequently occurs.

DISCUSSION: *G. multituberculatus* seems to be closely related to *G. ortizi. Gigantodax multituberculatus* has a pale reddish-brown female, the male is bright reddish orange, the sensory vesicle of the palp in both sexes is large, apertures in the tightly woven cocoon are absent, the divergent dorsal inner primary branch of the pupal gill has an origin of most secondary branches very close to the base of the gill, the facial trichomes (slender in *ortizi*) are stout and spinelike, and the platelets on the thorax are numerous but not formed into groups. The larvae are very similar, and we have been able to distinguish them only by the position of the branchings in the gill histoblast, which is close to the base of the gill in *multituberculatus* and more remote in *ortizi.*

Gigantodax patihuaycensis, new species
Figure 75A–M

DIAGNOSIS: *Gigantodax patihuaycensis* differs most recognizably from related species by the peculiar concentration of the platelets along the suture of the pupal thorax.

DESCRIPTION: *Female.* Not known.

Pharate male. Length of wings 4.0 mm. Color of antenna dark brown, scapus and pedicellus orange. Scutum dark reddish brown.

Holoptic. Shape and proportions of antennal segments as in figure 75F; ratio length/width of first flagellomere 1:0.53. Sensory vesicle of maxillary palp much longer than usual in the genus (fig. 69D, E), with distinct neck. Sc with 17–19 hairs. R with setae arranged in one or two irregular rows. R_1 with setae mostly in a single row; spinule present, beginning slightly basal to level of insertion of Sc on C, more numerous than interspersed setae (fig. 75A). R_s with setae in one row on apical half of upper, two rows on entire undersurface of vein. Shape and proportions of some leg segments as in figure 75B, G. Fore basitarsus 10.7 times, hind basitarsus 7.7 times as long as wide. Calcipala as in figure 75C. Genitalia without special characters. Distimere over two-thirds as long as basimere, with two apical spines; main body of ventral plate as long as wide.

Pupa. Cocoon consisting of shapeless bag formed by very loose, wide mesh, incrusted with mineral and organic detritus, extending over entire pupa except head and gills. Threads forming fabric of cocoon dark brown. Length of cocoon about 5.0 mm, of pupal exuviae 4.6 mm, cephalopterothecal length 2.5 mm. Gill with filiform, forwardly directed branches forming a tight, narrow bundle. Basal stalk of gill approximately three times as long as width on narrow portion (fig. 75J). Primary branches numbering four or five, only slightly diverging from direction of longitudinal axis of stalk. Terminal branches arising very closely to base of branched portion of gill. Total length of gill not less than 3 mm. Shape and proportions of frontoclypeus as in figure 75H. Surface of sclerite somewhat rugose, with very faint traces of isolated platelets. Facial trichomes stout, spinelike. Thorax with few but distinct smooth platelets, concentrated along dorsal suture and scattered on lateral portion of thorax (fig. 75I); area around dorsocentral trichomes completely bare. Dorsocentral trichomes consisting of two stout spinelike setae and one more slender set (not shown in illustration). Dor-

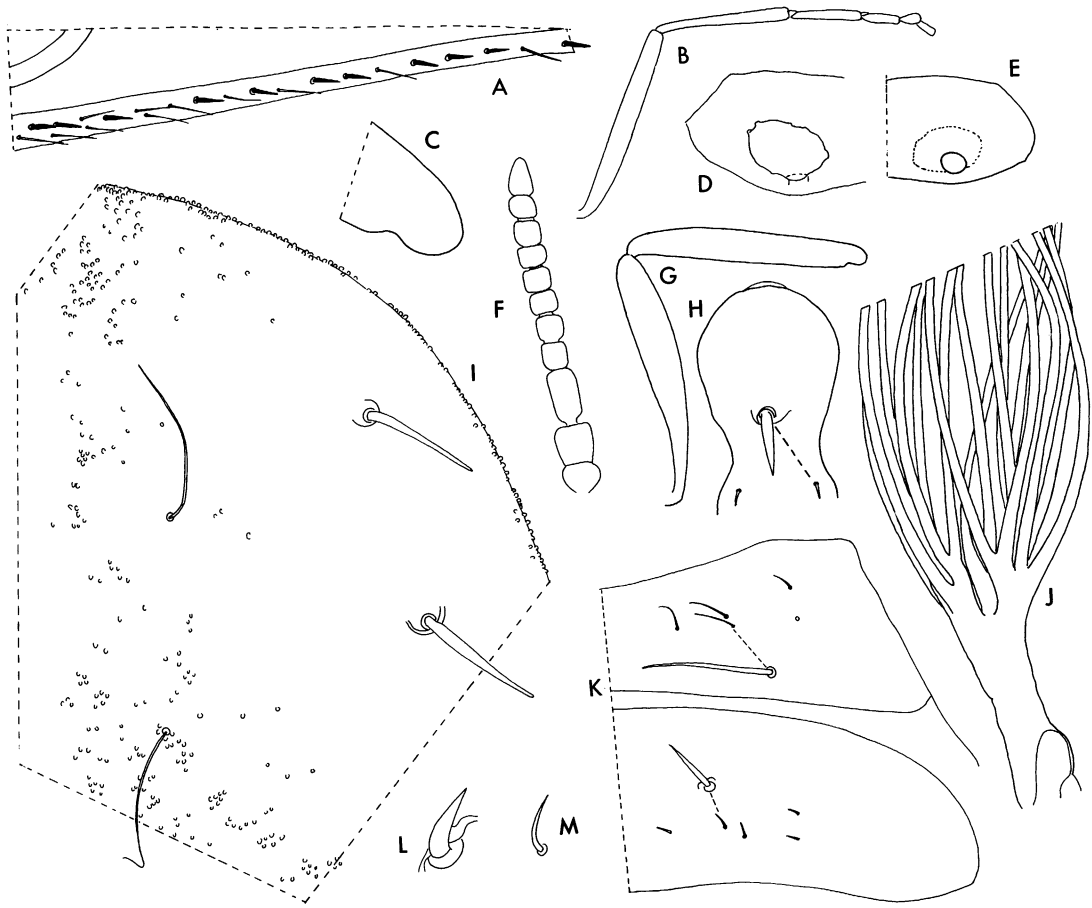

Fig. 75. *Gigantodax patihuaycensis.* Male. **A.** Anterior portion of wing. **B.** Foreleg, incomplete. **C.** Calcipala. **D, E.** Portion of second article of maxillary palp. **F.** Antenna. **G.** Hind leg, incomplete. **H.** Frontoclypeus of pupa. **I.** Portion of thorax, with trichomes. **J.** Basal portion of gill. **K.** Chaetotaxy of abdominal tergites I and II. **L.** Hook of tergite IV. **M.** Anterosublateral seta of abdominal tergite III.

solateral trichomes delicately hairlike. Setae of abdominal tergite I hairlike, elongate, their length 90 μm; setae of tergite II short, spinelike (fig. 75K), 32–40 μm long. Tergites III and IV each with 4 + 4 short but relatively stout hooks (fig. 75L); anterosublateral setae slender (fig. 75M). Setae of segments VI–VIII delicate, their length on tergite VII about 50 μm. Spine-combs on segments VI–VIII, short and interrupted, their number on tergite VII about 35, their length about 20 μm, viz., about half as long as setae of tergite VII. Specialized setae on segments VIII and IX from straight to variously curved, only very rarely branched. Sternite VI with several scattered hooklike setae; V with 3 + 3, sternal plate VI with 2 + 2, VII with 1 + 1 hooks, one hook each also in pleural membranes of segments VI and VII. Sternite VIII glabrous.

Larva. Not known.

HOLOTYPE: PERU: Patihuayco, 2300 m, Aug. 15, 1953 (A. Herrer; AMNH), pharate male, with associated pupal exuvia.

ETYMOLOGY: This species is named for Patihuayco, the Peruvian locality where it was collected.

DISCUSSION: The peculiar distribution of the platelets on the thorax, as described and illustrated above, is unique, and suffices to distinguish this species from all possibly re-

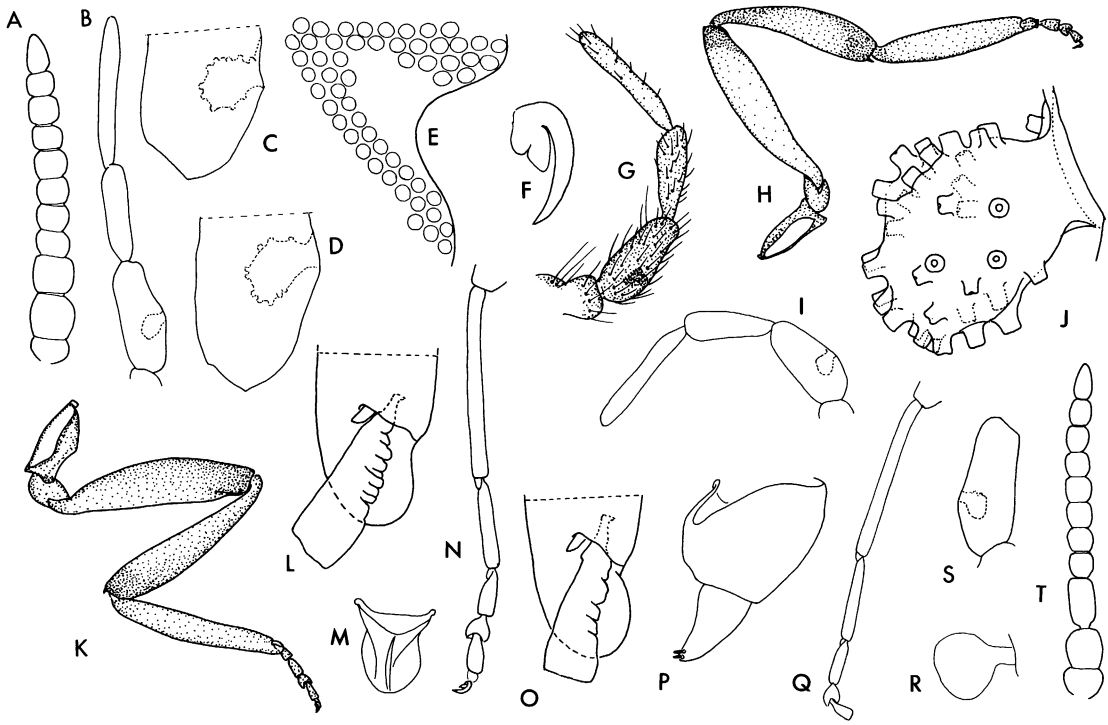

Fig. 76. *G. laevigatus.* A–F. Female. **A.** Antenna. **B.** Maxillary palp. **C, D.** Portion of second article of maxillary palp. **E.** Fronto-ocular triangle. **F.** Claw. G–J. Male. **G.** Maxillary palp. **H.** Hind leg. **I.** Maxillary palp. **J.** Sensory vesicle of second article of maxillary palp. **K.** Hind leg of female. **L.** Calcipala, with second article of basitarsus of female. **M.** Ventral plate of male genitalia. **N.** Tarsus of foreleg of female. O–S. Male. **O.** Calcipala with second tarsal segment. **P.** Basimere and distimere. **Q.** Tarsus of foreleg. **R.** Outline of sensorial vesicle. **S.** Second article of maxillary palp. **T.** Antenna.

lated ones. We have been unable to place the type locality, Patihuayco, nor has the collector himself. We suspect that the locality is in the Junin Department in the Rimac Valley.

Gigantodax laevigatus, new species
Figures 76A–T, 77A–K, 78A–G

DIAGNOSIS: *Gigantodax laevigatus* differs most recognizably from related species by the absence of platelets on the head and thorax of the pupa.

DESCRIPTION: *Female.* Length of wing 3.3–3.5 mm. Color as in *ortizi.* Frontal angle 55–60°. Shape and proportions of antennal segments as in figure 76A. Fronto-ocular triangle slightly higher than wide (fig. 76E). Mandible with approximately 24 teeth on inner margin only. Maxilla with about 30 teeth. Terminal segment of maxillary palp slightly less than 1.5 times as long as penultimate (fig. 76B). Second segment of maxillary palp suboval, ratio length/width = 1:0.45–0.53. Sensory vesicle comparatively small, suboval, with long neck (fig. 76C, D); Sc with 24–28 setae, extending to insertion of Sc on C. Setae on R in two irregular rows extending to base of R_1; further apicad on R_1 is a single row interspersed with spinules, beginning slightly basal to level of insertion of Sc on C; spinules about as numerous as interspersed setae. Setae on R_1 in one row on dorsoapical half of vein, in two or three irregular rows on entire length of undersurface of vein. Shape and proportions of some leg segments of fore and hind leg as in figure 76K, N. Hind basitarsus 7.3–7.4 times as long as wide. Calcipala extending well beyond middle of second tarsomere, but falling distinctly short of its apex (fig. 76L). Basal tooth of claw as in figure 76F.

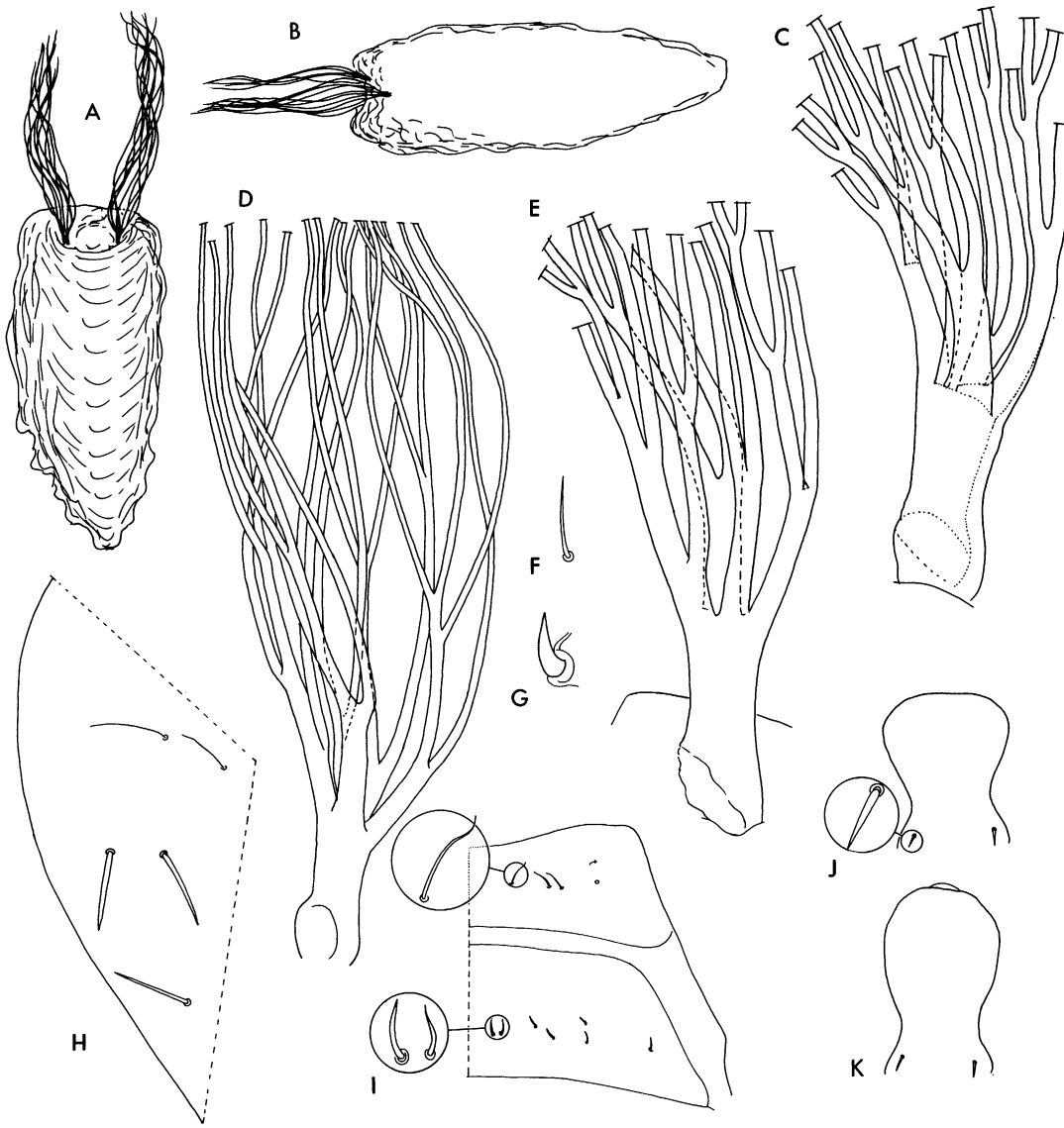

Fig. 77. *G. laevigatus.* Pupa. **A.** Pupa in cocoon, dorsal view. **B.** Same, lateral aspect. **C–E.** Basal portion of gills. **F.** Dorsolateral trichome of abdominal tergite III. **G.** Hook of abdominal tergite III. **H.** Portion of thorax, with trichomes. **I.** Chaetotaxy of tergites I and II. **J.** Frontoclypeus of female. **K.** Same, male.

Abdominal sterna with only delicate hairs. Genitalia as in *ortizi.*

Male. Length of wing 3.3–3.5 mm. Color as in *ortizi.* Holoptic. Shape and proportions of antennal segments as in figure 76T; ratio length/width of first flagellomere 1:0.56–0.71. Terminal segment of maxillary palp 1⅓ times as long as penultimate (fig. 76G). Sensory vesicle small, oval, with short, distinct neck (fig. 76J, R, S). Wing as in female, but Sc with 20–27 setae, not attaining apex of vein. Shape and proportion of some leg segments of fore and hind leg as shown in figure 76H, Q. Fore basitarsus 9.8–11.6 times as long as wide; hind basitarsus 5.6–5.7 times as long as wide. Calcipala in male extending closer to apex of second tarsomere (fig. 76O) than in female. Distimere over two-thirds as long as basi-

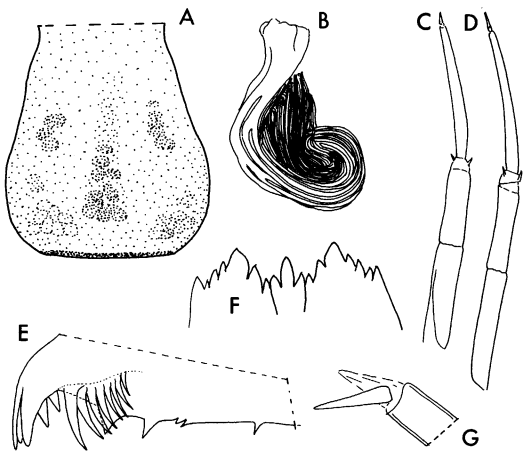

Fig. 78. *G. laevigatus.* Larva. **A.** Cephalic apotome. **B.** Gill histoblast. **C, D.** Antennae. **E.** Distal portion of mandible. **F.** Teeth of hypostomium. **G.** Apical sensilla of antenna, with "sheath."

mere, with two or three apical spines (fig. 76P). Main body of ventral plate about as long as wide (fig. 76M).

Pupa. Cocoon, when well preserved, completely covering body of pupa, and also basal portion of gills in some specimens (fig. 77A, B). Fabric of cocoon with very coarse, irregular mesh with wide apertures, its color dark brown. In most specimens examined cocoon encrusted with large amount of organic material. Length of cocoon 4–5 mm. Total length of body of pupa 2.8–3.0 mm; cephalopterothecal length 2.1 mm. Gill light brown, forwardly directed filiform branches (fig. 77A–E). Stalk of gills 2.5–3.0 times as long as wide on narrow portion. Arrangement of primary and secondary gill branches very similar to that of *ortizi.* Total length of intact gills not more than 3.0 mm. Shape and proportions of frontoclypeus of female and male as in figure 77J, K; surface slightly wrinkled, platelets absent. Facial trichomes short, spinelike. Thorax without platelets. Dorsocentral trichomes consisting of two stout and one thin seta varying from slender spinelike to hairlike; dorsolateral trichomes very delicate, hairlike (fig. 77H). Setae of abdominal tergite I hairlike, their length 43–60 μm; setae of tergite II short and stout, their length 28–32 μm (fig. 77I). Tergites III and IV each with 4 + 4 short hooks (fig. 77G). Dorsolateral setae (fig. 77F) slender, about as long as hook. Setae of tergites VI–VIII slender, length on tergite VII 30–40 μm. Spine-combs on tergites VI–VIII continuous or with slight interruptions, consisting on tergite VII of 34–38 spines, length 18–20 μm, viz., not less than one-half as long as setae of this tergite. Sternite IV with thin or strong but not hooklike setae; V with 3 + 3, sternal plates VI with 2 + 2, and VII with 1 + 1 hooks, one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 6.5–7.5 mm, width of head capsule 0.7 mm. Body shape as usual for the genus; ventral papillae present. Almost entire body with faint but distinct hypodermal pigment, most intense on posterior portion of body. Head light brown; spots of cephalic apotome from distinct to blending into background (fig. 78A). Hypostomial bridge region not distinctly darker than rest of head, with very faint median longitudinal line whitish. Antenna as long as or slightly longer than stem of cephalic fan, faintly pigmented, third segment darkest. Shape of antenna as in figure 78C, D; ratio of segments I–III = 1:0.61–0.67:1.2–1.25. Terminal sensillum four times as long as wide at base, with faintly perceptible, elongate, lamellar structure (fig. 78G). Cephalic fan with 30–35 large rays, their teeth as in *ortizi.* Mandibles (fig. 78E) with seven to nine inner teeth and five to eight marginal serrations. Maxillary palp about 2.5 times as long as wide. Hypostomium (fig. 78F) and cervical sclerites as in *ortizi.* Gill histoblast as in figure 78B. Color of mature gill histoblast light brown, base even lighter. Perianal scales and recurrent struts as in *ortizi.* Crochet ring with 85–90 rows of approximately 20 hooks each. Recurrent struts well developed.

HOLOTYPE: ECUADOR: *Cotopaxi:* NW slope of Mt. Cotopaxi, 3500 m, July 26–Aug. 5, 1969 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female allotype, 11 males, 12 females, paratypes (all reared, and with their associated pupal exuviae), pupae, and larvae. ECUADOR: *Pichincha:* road from Quito to Papallacta, 3300 m, July 20–Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), 2 males, 3 females, paratypes (all reared, and

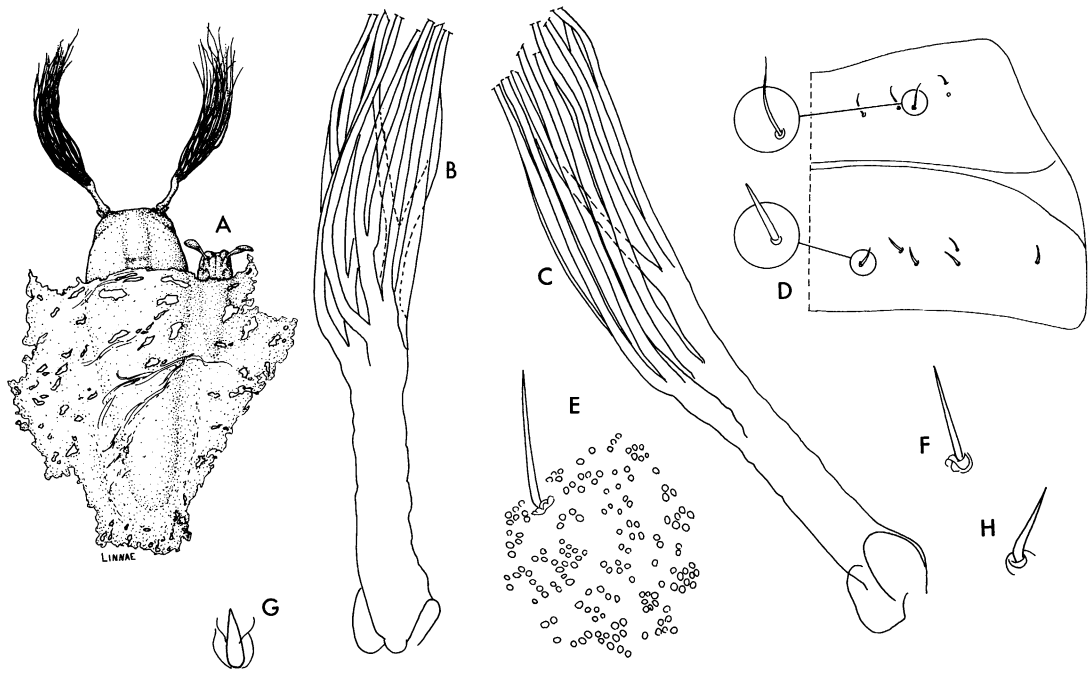

Fig. 79. *Gigantodax zumbahuae.* **A.** Pupa in cocoon. **B, C.** Basal portion of gills. **D.** Chaetotaxy of abdominal tergites I and II. **E.** Detail of thorax, with trichomes. **F.** Facial trichome. **G.** Hook of abdominal tergite IV. **H.** Anterodorsal trichome of thorax.

with their associate pupal exuviae), pupae, and larvae; San Juan, Paramo de Guamani, on Quito-Papallacta road, 3700 m, Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal exuviae), pupae, 1 larva.

ETYMOLOGY: The specific name is taken from the Latin *laevigatus,* smooth, an allusion to the absence of platelets on the head and thorax of the pupa.

BIOLOGY: The species was collected at elevations of 3000 m and higher, in small streams with rocky bottoms, not over 30 cm wide and 10 cm deep, and with temperatures of approximately 10°C. Pupae were found mainly on the undersides of watercress leaves, trailing grass, and other vegetation; only occasionally on the undersides of stones. In many cases, pupae formed irregular aggregations, especially on grass blades. Pupae on watercress leaves were in most cases one per leaf, rarely two or three.

DISCUSSION: *Gigantodax laevigatus* is very closely related to *G. ortizi* with which it shares such characters as the dark brown color of the scutum of the male, the small sensory vesicle of the female palp, the wide male posterior basitarsus, the elongate primary gill branches, and the wide apertures of the cocoon. The color of the female scutum is dark purple in *ortizi* and light brown in *laevigatus.* The frontal angle of the female of *laevigatus* (55–60°) is distinctly larger than in any other species of the group, and the complete absence of platelets on head and thorax of the pupa is probably a derived character.

Gigantodax zumbahuae, new species
Figure 79A–H

DIAGNOSIS: *G. zumbahuae* differs from related species by the very long pupal gill stalk.

DESCRIPTION: Female and male unknown.

Pupa (female). Cocoon (fig. 79A) in form of shapeless bag, not covering anterior portion of thorax. Fabric of cocoon with numerous apertures. Total length of pupa 4.6 mm; cephalopterothecal length 2.6 mm. Gills light brown, forwardly directed branches forming an extremely tight bundle (fig. 79A–C). Basal stalk of gill 5.0–5.3 times as long as wide on main portion. Primary branches

numbering four or five, continuing, as do secondary branches, in same direction as longitudinal axis of basal stalk. Secondary branches in most cases branching off dichotomously at moderate distance from base of gill. Total length of intact gill 3 mm. Structure of gill branches as in *ortizi.* Platelets of frontoclypeus smooth, numerous, forming irregular pattern similar to that of thorax. Facial trichomes in shape of slender spine (fig. 79F). Thorax with platelets smooth (fig. 79E); dorsolateral trichomes very slender, hairlike. Setae of abdominal tergite I (fig. 79D) hairlike, their length 80–95 μm. Tergites III and IV each with 4 + 4 short hooks (fig. 79G). Anterodorsal setae (fig. 79H) stout, as long as or longer than hooks. Setae of tergites VI–VIII slender, comparatively short. Spinecombs of tergites VI–VIII, very irregular, with several short interruptions, consisting on tergite VII of 33 spines, their length 30–40 μm, viz., over half as long as setae of this segment. Specialized setae of segments VIII and IX straight or slightly curved, not branched. Sternite IV with conspicuous isolated hooklike setae; sternite V with 3 + 3, sternal plate VI with 2 + 2 and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Larvae. Unknown.

HOLOTYPE: ECUADOR: *Cotopaxi:* Road from Pujili to Quevedo, Rio Zumbahua, 3500 m, July 29–Aug. 15, 1969 (P. and B. Wygodzinsky; AMNH), pupa.

ETYMOLOGY: The specific name is taken from that of the river in which this insect was found.

BIOLOGY: The stream where it was collected, with its wide bed and rocky bottom, is very different from the watercourses (described under the heading of *G. ortizi*) where other related species occur.

DISCUSSION: Although this species is represented in our material by a single pupa, we feel that its unique characters warrant a formal description and naming. The most outstanding morphological feature of *G. zumbahuae* is the elongate stalk of the pupal gills, combined with the very tight bundle formed by the branches of the gill. This is the only species of the *brophyi* group we found in the western Cordillera of the central valley of Ecuador. Both *multituberculatus* and *laevigatus* were collected in considerable quantities, but only in the eastern Cordillera.

cilicinus group

DIAGNOSIS: Recognized by the basally thickened gill branches, with thin and deciduous filaments distally, frequently with branch numbers 12 and 16 (exceptionally 15) longer than the others, and mostly with tegumentary processes; female claw with the subbasal tooth subtriangular.

FEMALE: Medium-size to large species, from orange to dark purple. Morphology of body and appendages and genitalia very close to *brophyi* group. Subbasal tooth of female claw subtriangle in shape, from short (figs. 94I, 99E) to very elongate (figs. 89G–I); spinules on R_1 present.

MALE: Morphology similar to *brophyi* group.

PUPA: Cocoon generallly not well developed. Gill with generally 17–18 branches thickened basally with branches 12 and 16 (rarely 12 and 15) more elongate, with thin apical caducous filament, and from smooth to incipient or well-developed hairlike cuticular processes. Trichomes of frontoclypeus and thorax not apically hooked. Abdominal I with 3–5 + 3–5 thin trichomes of similar shape; terminal hooks stout.

LARVA: Cephalic apotome widest near base; antenna as long as stem of cephalic fan; terminal sensillum variable, from medium to elongated (ratio length/width = 1:3.5–6.0). Ratio of antennal segments normal. Mandible with numerous marginal serrations (6–17). Hypostomium with median tooth short to very long (figs. 83G, 103L). Recurrent struts generally well developed. Anal scales forming a complete circumanal ring. Anal gill with three simple lobes.

DISTRIBUTION: From Colombia to the northern Patagonian Andes (fig. 109).

DISCUSSION: This is a heterogeneous group of 11 species in which we include tentatively two poorly known species: *mariobordai* and *incomitatus.* Only three, *arrarteorum, cilicinus,* and *clandestinus,* have several derived character states showing unquestionable relationships, such as the following: stout sub-

triangular shape of the subbasal tooth of the claw (fig. 99E), mandibles weakly crenulate on the external border (fig. 99B), presence of a small fronto-ocular triangle in males (fig. 99O), gill tubular branches tapered abruptly and projected with a caducous filament, and presence of long hairy cuticular processes (fig. 101B, C), well pigmented larval head (fig. 103B, C), distinctly elongated median and fourth lateral hypostomial teeth (fig. 103L), and many marginal serrations on the larval mandible (fig. 103I).

The presence of fronto-ocular triangles in males and the elongate median tooth and four lateral teeth of the larval hypostomium as seen in the most primitive *Gigantodax* groups, are not considered synapomorphic here. Here the fronto-ocular triangle is smaller than in the primitive condition, and the median tooth is shorter, with first intermediate teeth below the corner teeth.

The short subtriangular shape of the subbasal tooth of the claw probably is derived from a subrhomboidal or elongate subtriangular shape, but a scanning electron microscope study of the claws is needed to accurately define shape variation and types.

Among the other species *pennipunctus* is the closest to this peculiar subgroup, possessing the same type of claw tooth and also having rudimentary tegumentary process on the gill branches (fig. 96E).

Remaining species of this group (*basinflatus, destitutus, fulvescens,* and *shannoni*) have in common with the typical species cited above a subtriangular claw tooth and very thin apical filaments of gill branches, a few of which are sclerotized and easily detached. *Gigantodax destitutus* and *G. shannoni* have branches 12, 15, and 16, respectively, elongated. Sixteen gill branches also occur in higher species of *Gigantodax,* as described below.

Gigantodax basinflatus and *G. mariobordai* have swollen basal gill branches, which is a character state shared with the typical *cilicinus* group species.

The *cilicinus* group is subdivided into three subgroups: (a) *basinflatus* + *destitutus* + *incomitatus* + *mariobordai* + *shannoni*; (b) *pennipunctus*; and (c) *arrarteorum* + *cilicinus* + *clandestinus.*

Gigantodax fulvescens (Blanchard)
Figures 81A–Y, 82A–J, 83A–O

Simulium fulvescens Blanchard, 1852: 353.
S. (Gigantodax) fulvescens: Edwards, 1931: 137.
Gigantodax fulvescens: Wygodzinsky, 1961a: 460; 1961b: 563. Vulcano, 1967: 3; 1977: 290.

DIAGNOSIS: Thorax and legs yellowish and abdomen light gray brown, calcipala about two-thirds length of tarsomere 2; with spines on R_1. Pupal gill with filamentous branches, relatively flattened frontally in side view.

REDESCRIPTION: *Female.* Wing length 3.5–3.7 mm. Head blackish, eyes black, antennae light yellow brown, basal article orange; frons, clypeus, maxillary palp, and occiput gray brown with gray pollinosity; setae on antenna, frons, maxillary palp, and occiput silvery to golden. Scutum, scutellum, metanotum, pleuron, and legs pale yellow to golden. Wing hyaline, membrane vein light brown, hairs yellow to brown, spinules dark brown. Abdomen brown with posterior border of tergites yellow gray; hairs of first abdominal terga golden yellow.

Frons shape close to *antarcticus*; fronto-ocular triangle wider than high (fig. 81O). Antenna as in figure 81N. Maxillary palp with second article stout (fig. 81P, ratio length/width = 1:6.6–7.1; sensory vesicle about half width of basal article, with abundant tuberosity (fig. 81L). Mandible with 30 and maxilla with about 25 teeth. Structure of setae of scutum and scutellum as in *antarcticus.* Wing chaetotaxy very close to *marginalis* but with fewer spinules on R_1. Shape, proportion, and distribution of pigment on fore and hind legs as in figure 81S–U. Ratio length/width of hind basitarsus about 6.0 (fig. 81 T). Calcipala covering approximately two-thirds of second tarsomere (fig. 81W). Claws as illustrated in figure 81Q. Genitalia as in figure 81V, X, Y. Eighth sternite with about 20 + 20 setae; gonapophyses with 5–7 setae and abundant microtrichiae, cercus with straight border. Spermatheca as in *G. brophyi.*

Male. Wing length 3.5–3.7 mm. Coloration as in female but more strongly yellow, especially the nearly orange scutum; abdomen brownish, darker than in female, abdominal setae from golden to light brown. Shape of antennal articles as in figure 81A,

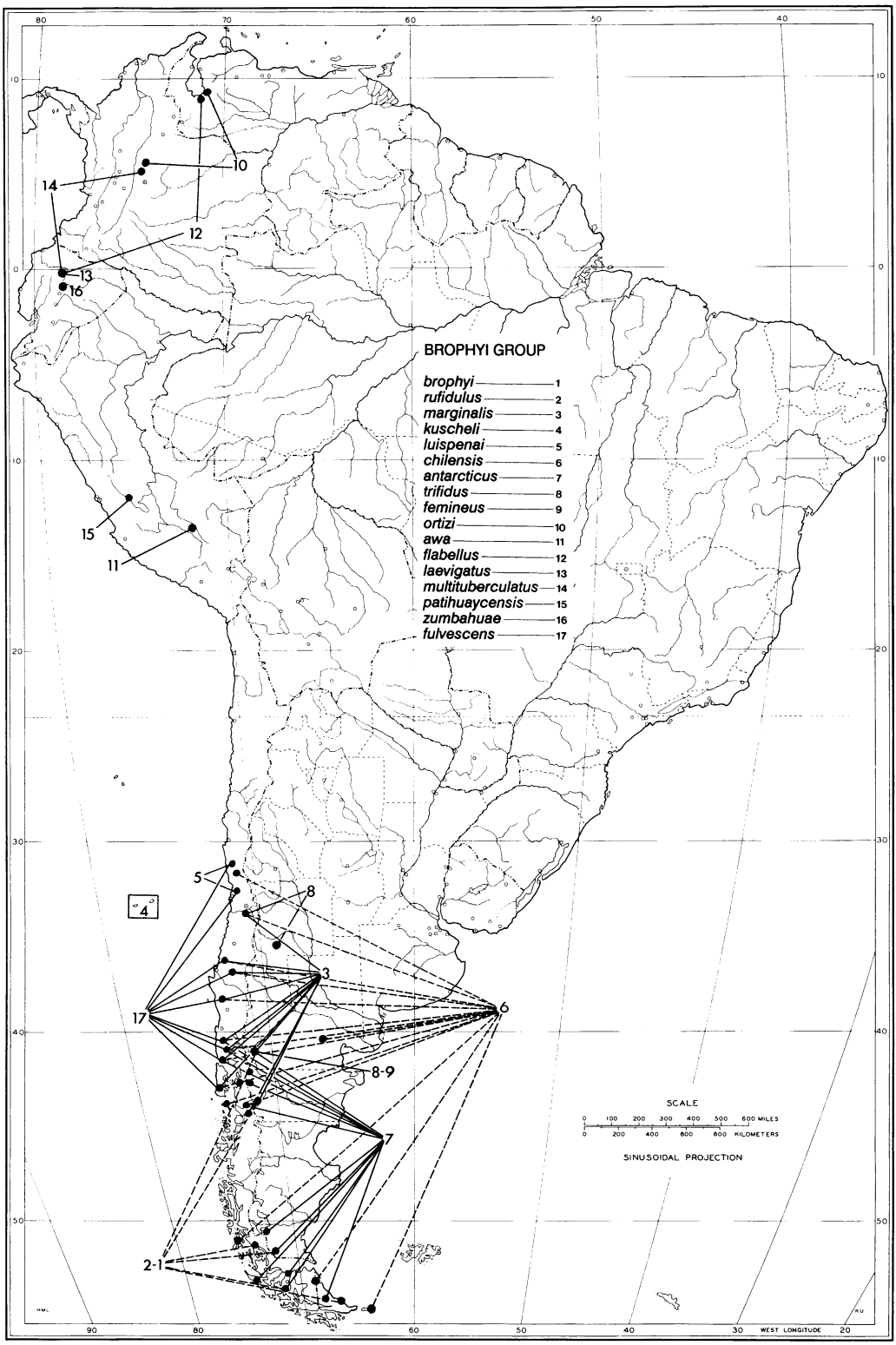

Fig. 80. Map with the distribution of species of *brophyi* group.

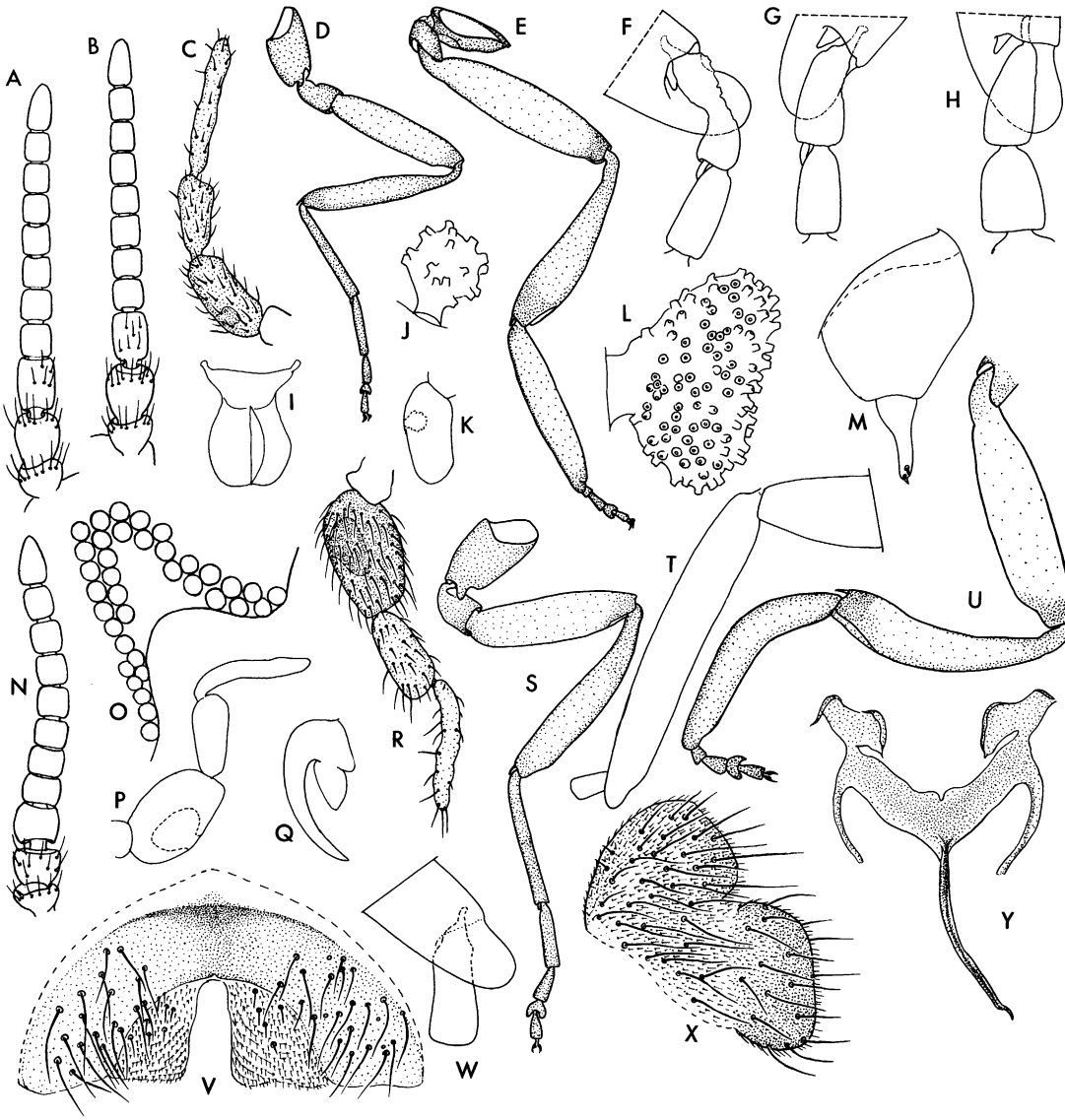

Fig. 81. *Gigantodax fulvescens.* **A.** Antenna of male. **B.** Same, female. C–G. Male. **C.** Maxillary palp. **D.** Foreleg. **E.** Hind leg. **F, G.** Calcipala, with second tarsal segment. **H.** Same, female. **I.** Ventral plate. **J.** Sensory vesicle of maxillary palp of male. **K.** Second segment of maxillary palp of male. **L.** Sensory vesicle of second segment of maxillary palp of female. **M.** Basimere and distimere. N–Y. Female. **N.** Antenna. **O.** Fronto-ocular triangle. **P, R.** Maxillary palpi. **Q.** Claw. **S.** Foreleg. **T.** Posterior basitarsus. **U.** Hind leg. **V.** Eighth sternite and gonapophyses. **W.** Calcipala, with second tarsal segment. **X.** Cercus and paraproct. **Y.** Genital fork.

B. Maxillary palp with basal article about two times as long as wide (fig. 81C); sensory vesicle less than half the length of basal article (fig. 81J, K). Wing as in female. Shape, proportion, and distribution of pigmentation on fore and hind legs as in figure 81D, E. Calcipala longer than wide and about two-thirds length of second tarsomere (fig. 81F–H). Ratio length/width posterior basitarsus 5.0–5.5.

Genitalia very close to *G. antarcticus,* but endoparamere hooks proportionally shorter and stouter. Distimere with two apical spines, length about half that of basimere (fig. 81M). Ventral plate as in figure 81I.

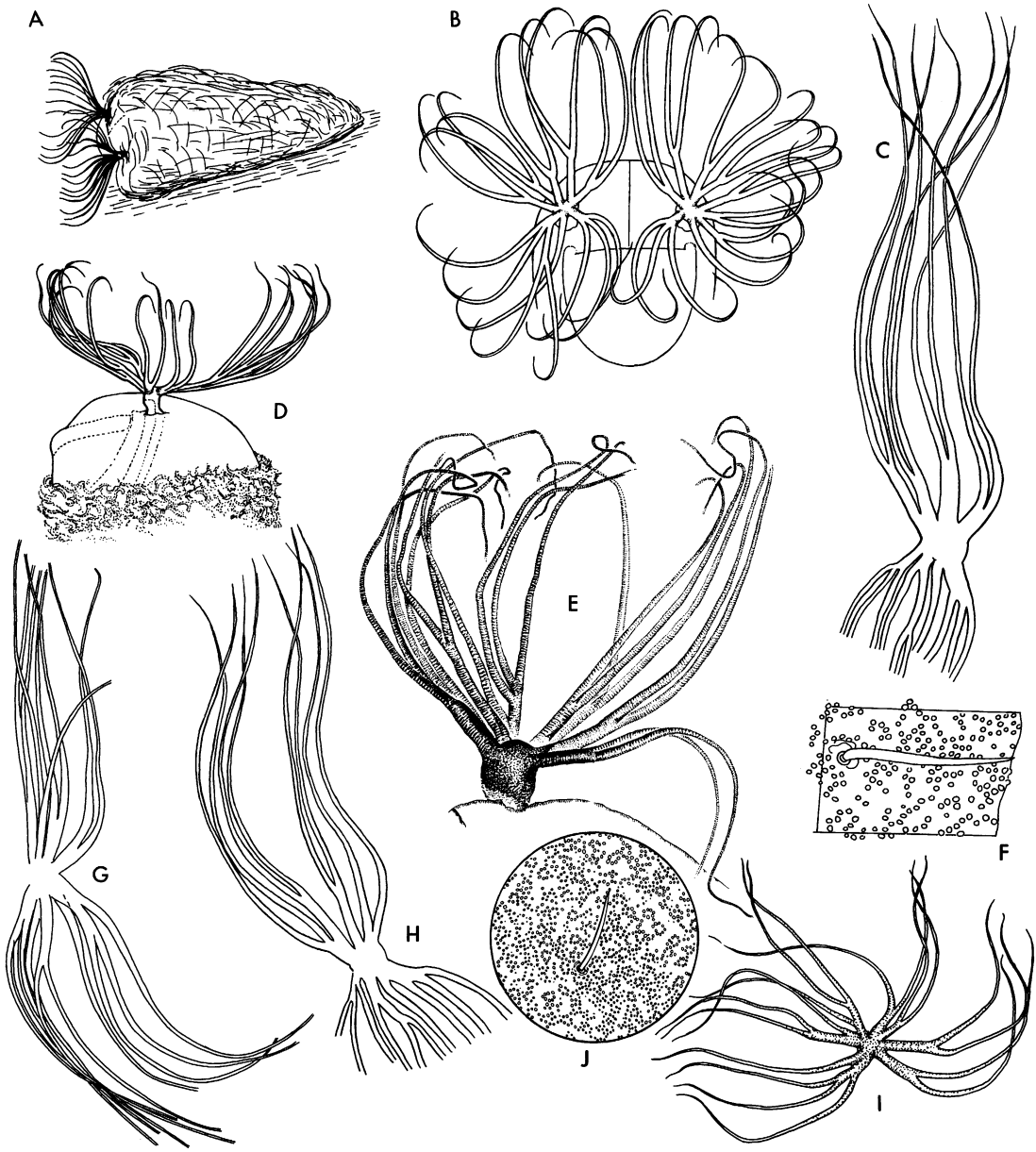

Fig. 82. *G. fulvescens.* **A.** Pupa in cocoon, side view. **B.** Pupa, front view. **C.** Portion of gill. **D.** Head of pupa, side view. **E.** Gill. **F, J.** Trichomes and platelets of thorax, different magnifications. **G–I.** Different gills.

Pupa. Cocoon with irregular shape (fig. 82A), covering the body and base of gills. Mesh threads irregular, with small sandy particles adhering. Cocoon length at base 4.0–4.5 mm; body length 3.5–4.0 mm; cephalopterothecal length 2.5–2.9 mm. Maximum length of gill filaments 1.5 mm. Gill with filaments distally very thin and easily detached; gill branches generally very open basally giving side view flattened aspect, with small curvature distally (fig. 82A, D); some specimens with variable disposition as shown in figures 82C, E, G–I, 83M, N. Frontoclypeus and thorax light brown with abundant platelets,

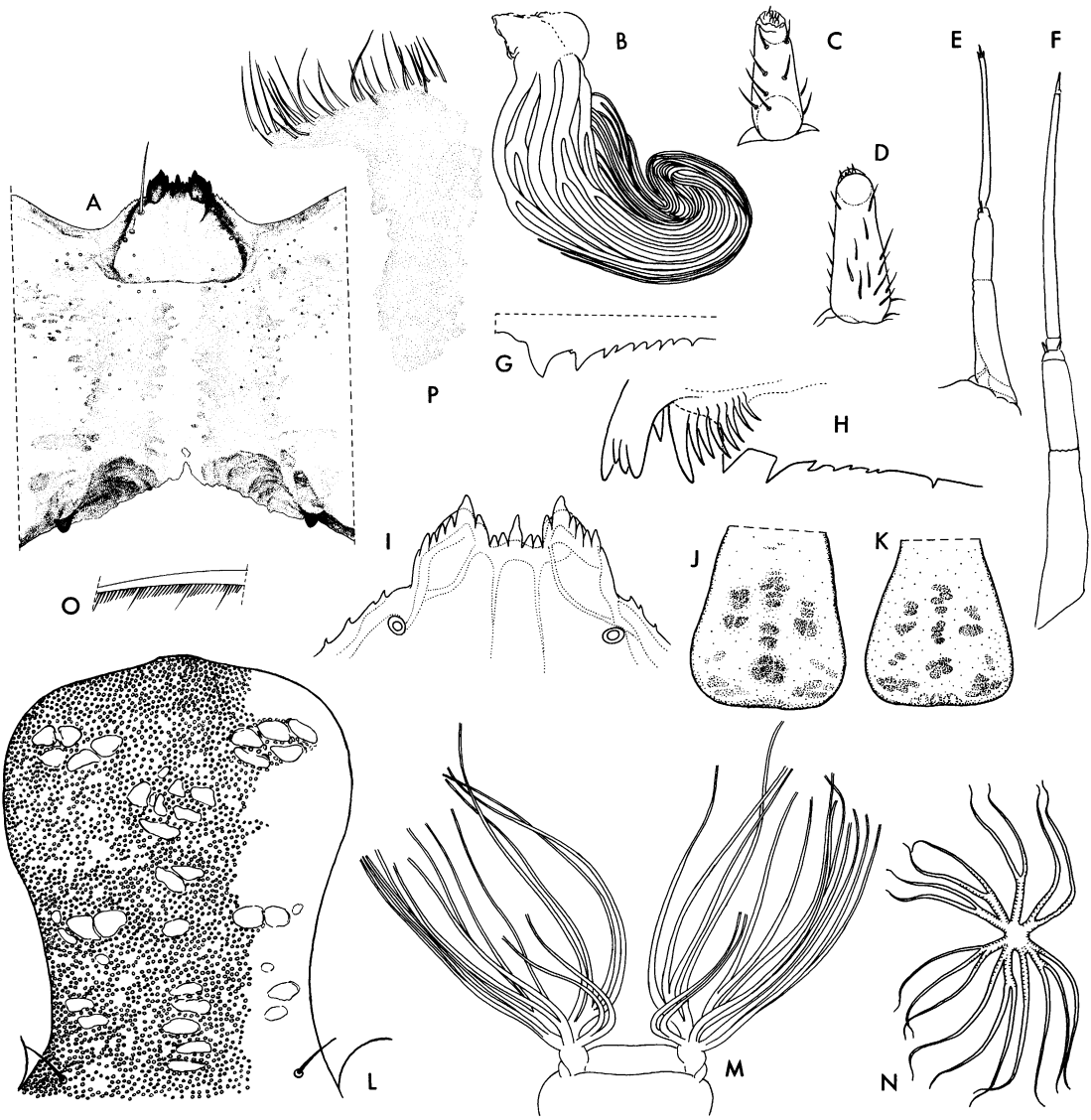

Fig. 83. *G. fulvescens.* A–K. Larva. **A.** Hypostomial bridge. **B.** Gill histoblast. **C, D.** Maxillary palp of different specimens. **E, F.** Antennae. **G.** Marginal serrations of mandible. **H.** Apex of mandible. **I.** Hypostomium. **J, K.** Cephalic apotome of larva. **L.** Frontoclypeus of male with platelets. **M.** Anterior portion of body with gills, dorsal view (El Canelo). **N.** Gill, frontal view.

mostly rugose (figs. 82F, J, 83L), frequently arranged in circles, especially on thorax. Chaetotaxy of head, thorax, and abdomen as in *antarcticus.*

Larva. Maximum length 7.0 mm, maximum width of cephalic capsule 0.65–0.70 mm. Body color light greenish brown, head light brown ventrally with 1 + 1 wide submedian irregular bands, darker on the hypostomial bridge (fig. 83A). Cephalic apotome ornamented as in figure 83J, K. Antenna as long as, or shorter than, stem of cephalic fan. Antenna with third article very long (fig. 83E, F), ratio of articles I–III as 1:0.6–0.7: 1.4–1.6, terminal sensilla 4–5 times as long as wide at base. Ratio of length/maximum width of maxillary palp 2.3–2.7 (fig. 83C, D). Mandible with 8–12 internal teeth, and 7–11

marginal serrations (fig. 83G, H). Cephalic fan with 30–38 rays, tooth rays arranged as in figure 83O. Hypostomium with median tooth below level of corner teeth, and about same level as external teeth (fig. 83I). Sclerite of proleg with 29–36 teeth. Anal sclerite with abundant scales at base; crochet ring with 92–114 rows with 19–24 hooks in each row. Gill histoblast as shown in figure 83B.

MATERIAL EXAMINED: ARGENTINA: *Chubut:* Creek near Lake Futalaufquen, Jan. 13, 1962 (S. Coscarón; MLP), pupa; Puerto Limonao on Lake Futalaufquen, Jan. 12, 1962 (S. Coscarón; MLP), 1 male (with pupal exuviae), pupae, and larvae; creek near Lake Futalaufquen, Feb. 3, 1975 (S. Coscarón; MLP), pupae, and larvae. *Rio Negro:* Bariloche, Nov. 3–10, 1926 (Shannon; USNM), 1 male, det. Edwards; Bariloche, Dec. 1, 1926 (Shannon; USNM), 1 male, det. Edwards; Bariloche, Nov. 20–30, 1926 (Shannon; CNC), 1 male, det. Edwards; Bariloche, Nov. 28, 1957 (Flapo-Bahr; AMNH), pupa; Bariloche, Nov. 25, 1950 (P. Wygodzinsky; AMNH), 2 males (with pupal exuviae), 1 male, pupa; Bariloche, Arroyo Michay, Jan. 22, 1971 (S. Coscarón; MLP), pupae and larvae; Bariloche, Arroyo Pilmaiquen, Jan. 28, 1971 (S. Coscarón; MLP), pupae and larvae; Bariloche, chorrillo near Arroyo La Virgen, Jan. 22, 1971 (S. Coscarón; MLP), pupae and larvae; same, Apr. 10, 1983, pupae and larvae; Bariloche, Colonia Suiza, Nov. 27, 1975 (S. Coscarón; MLP), pupae and larvae; Bariloche, Arroyo los Notros, Jan. 17, 1983 (S. Coscarón; MLP), pupae and larvae; Playa Bonita, March 10, 1984 (M. Gentili; MLP), pupae and larvae; base of Cerro Lopez, Sept. 27, 1975 (S. Coscarón; MLP), 1 male with pupal exuviae, pupae, and larvae; same, Feb. 17, 1973, pupae and larvae; Feb. 9, 1975, pupa and larvae; creek in Valle de los Vuriloches, near Cerro Tronador, Oct. 22, 1970 (S. Coscarón; MLP), one pharate male, pupae, and larvae; Lago Gutierrez, Feb. 17, 1967 (S. Coscarón; AMNH), pupae; same, Chorillo near Hotel Tronador, Jan. 18, 1983 (S. Coscarón; MLP), pupae and larvae; Jan. 23, 1971, pupae. *Neuquen:* 5 km S of La Lipela, Nov. 25, 1975 (S. Coscarón; MLP), pupae and larvae; Confluencia, Oct. 25, 1970 (S. Coscarón; MLP), pupae; Arroyo Chacabuco, Feb. 16, 1967 (S. Coscarón; AMNH), pupae; small stream, 3 km S of crossing of Rio Alumine by route d, Oct. 25, 1970 (S. Coscarón; MLP), pupae and larvae; Arroyo Hua-Hum, Jan. 29, 1979 (S. Coscarón; MLP), 1 pupa; small stream in Hua-Hum, Jan. 23, 1980, pupae; Ruca Malen, Jan. 20, 1983 (S. Coscarón; MLP), larvae and pupae; 5 km S La Lipela, Sept. 25, 1975 (S. Coscarón; MLP), pupae; San Martin de los Andes, base of Cerro Chapelco, Jan. 21, 1978, pupae; Arroyo Chapelco Grande, Jan. 9, 1979 (S. Coscarón; MLP), pupae; Arroyo Quilanlahue, Jan. 22, 1978 (S. Coscarón; MLP), pupae; creek N Lago Lacar, Jan. 22, 1978 (S. Coscarón; MLP), pupae; creek near Arroya Partido, Jan. 23, 1978 (S. Coscarón; MLP), pupa and larvae; creek in Puesto Chiridiale, Jan. 23, 1980 (S. Coscarón; MLP), one pupa and larvae; Arroyo Hua-Hum, Jan. 29, 1979 (S. Coscarón; MLP), pupae; Yuco (Gentili; MLP), Jan. 8, 23, 1980, Feb. 2, 1982, pupae; Quiltrahue, Jan. 25, 1980, Apr. 1, 1979 (Gentili; MLP), pupae. CHILE: *Chiloe:* Ancud, Nov. 1926 (Shannon; USNM), 1 male (det. by Edwards); Chonchi, Feb. 7, 1967 (S. Coscarón; AMNH), pupae; Dalcahue, Feb. 1–8, 1962 (L. Pena; CNC), 3 males. *Llanquihue:* Casa Pangue, Dec. 1926 (Shannon; USNM), 1 male (det. by Edwards). *Osorno:* Parque Puyehue, Feb. 5, 1967 (S. Coscarón: AMNH), 1 female (with pupal exuviae), pupae, and larvae. *Valdivia:* Pucon, Feb. 1, 1967 (S. Coscarón; AMNH), 4 males (with pupal exuviae), pupae, and larvae. *Cautin:* Temuco, Feb. 1, 1967 (S. Coscarón; AMNH), 1 female (with pupal exuviae). *Malleco:* Rio Blanco, 1100–1200 m, Feb. 1964 (L. Pena, CNC), 2 males; Sierra de Nahuelbuta, W of Angol, Jan. 3, 1951 (Ross and Michelbacher; CAS), 3 males, 7 females; Angol, Oct. 18, 1931 (Bullock; USNM), 4 males. *Concepcion:* Oct. 1927 (USNM), 1 male; Escuadron, Oct. 13, 1972 (S. Coscarón; MLP), larvae. *Nuble:* 40 km E of San Carlos, Dec. 23, 1950 (Ross and Michelbacher; CAS), 1 female; Las Trancas, Termas de Chillan, 1270 m, Jan. 28, 1967 (Schlinger; CIS), 1 male, 1 female. *Linares:* Las Cruces, Oct., 1958 (L. Pena; CNC), 1 female. *Talca:* W of Alto de Vilches, 650 m, Jan. 13, 1967 (Schlinger; CIS), 5 males; Alto de Vilches, Oct. 5, 1972 (S. Coscarón, L. Pena, P. Wygodzinsky; AMNH), 1 male (with pupal exuviae), pupae. *Curico:* Estero La Junta, Jan., 1964 (L. Pena; CNC), 8 fe-

males; El Coigual, Jan. 20–26, 1964 (L. Pena; CNC) 2 females; Cajon del Rio Claro, 1200 m (Schlinger; CIS), 25 males, 4 females; Cajon del Rio Claro, SE of los Quenes, 1000 m, Jan. 10, 1967 (Schlinger; CIS), 12 males, 2 females, larvae. *O'Higgins:* Bosque de los Conservadores, Graneros, 1100 m, March 1–4, 1962 (L. Pena; CNC), 7 males, 6 females; Coya, Oct. 9, 1967 (S. Coscarón; AMNH), 1 male with pupal exuviae; small stream near Coya, Oct. 9, 1967 (S. Coscarón; AMNH), 1 pupa and larva. *Santiago:* Cuesta la Dormida, 1270 m, March 1, 1966 (Schlinger; CIS), 1 male; Cajon del Maipo, El Canelo, Oct. 1, 10, 1966 (Schlinger; CIS), 7 males; El Canelo, Dec. 4, 1963 (F. Edmunds; CNC), 4 males; El Canelo, Nov. 1, 1967 (S. Coscarón; AMNH), 1 female (with pupal exuviae); 4 females, 4 males mounted on slides, larvae, and pupae; Marga Marga, Nov. 27, 1927 (Shannon?; USNM), 2 males; El Alfalfal, Los Maitenes, 1800 m, Oct. 10, 1972 (L. Pena and P. Wygodzinsky; AMNH), 2 males (with the pupal exuviae), pupae; El Alfalfal, Rio Toro, 1300 m, Oct. 10, 1972 (L. Pena, P. Wygodzinsky; AMNH), 6 males, 3 females (with pupal exuviae), pupae; El Alfalfal, Oct. 12–13, 1969 (Flint and Barria; USNM), 1 male. *Valparaiso:* Rio Marga Marga, Los Perales, 33°09'S, 71°19'W, 330 m, Oct. 10, 1966 (Irwin-Schlinger; CIS), pupae, and larvae (larva parasitized by mermithids); Olmue, Oct. 9, 1967 (S. Coscarón; AMNH), 1 pupa. *Coquimbo:* Hacienda Illapel, Nov. 6, 1954, 1800 m (L. Pena; CNC), 6 males; Las Hedionditas, 2600 m, Oct. 25, 1967 (S. Coscarón; AMNH), larvae; International Highway to San Juan, 2500 m (S. Coscarón; AMNH), Oct. 26, 1967, pupae and larvae; Hacienda Illapel, El Calabazo, 1200 m, Oct. 26, 1967 (S. Coscarón; AMNH), pupae and larvae.

BIOLOGICAL INFORMATION: *Gigantodax fulvescens* breeds in small creeks of clear and cold waters, attached to rocks and leaves of tree branches. It is frequently found with *G. marginalis* and *G. chilensis.*

DISCUSSION: No type was designated by Blanchard, but we have been able to examine a series of four female specimens of *Gigantodax* from the collections of the Paris Museum, labeled as being from "Chile" and bearing the name Gay, accompanied in three specimens by the label "1843" and in one by "15-43." One specimen bears an additional label "*Simulium fulvescens* Bl."; this obviously old label is handwritten but not in Blanchard's handwriting, as illustrated by Horn and Kahle (1936, pl. 22, fig. 35). Although not well preserved, the specimens allowed us to see that coloration is in accordance with the original description, and to examine certain key characters, such as the structure of the hind legs (fig. 81T) and claws, and the wing length, although not the chaetotaxy. We are reasonably certain that the four females are conspecific, and that the specimens enumerated in this paper are conspecific with the specimens in the Paris Museum, which may be part of the original series upon which Blanchard based his species. Specimens kept in the British Museum and determined as *fulvescens* by Edwards coincide well with our material.

The yellow-orange-colored female and male are easy to confuse with *rufescens* and *shannoni,* but both are larger, the abdomen is more yellowish, the ratio of lengths of the calcipala and second tarsite is different, and the pupae have very different gills. Females and males of *G. minor* and *G. marginalis* could be confused too, when specimens of *fulvescens* are stained. The female of *minor* is easy to separate by the structure of the claws, but this does not work with *marginalis. G. chilensis* also is close but it is darker than the wing membrane is fumose. The flattened pupal gill is the best character for separation from other species with 18 branches. Larvae of *G. fulvescens* have two peculiar irregular dark stripes on the submentum and a relatively low-angle tooth that permit differentiation from other austral species.

G. fulvescens shows population variation in color and size. This is very evident in specimens from Santiago and Valparaiso provinces, these being relatively larger and light colored, but not consistently different enough to warrant separation as a different species. This species is one of the more common ones in central Chile and Patagonian areas, especially in summer.

G. fulvescens has three characteristics autapomorphic in relation to the previously described species of the *brophyi* group: pupal gill filaments distally very thin and few scler-

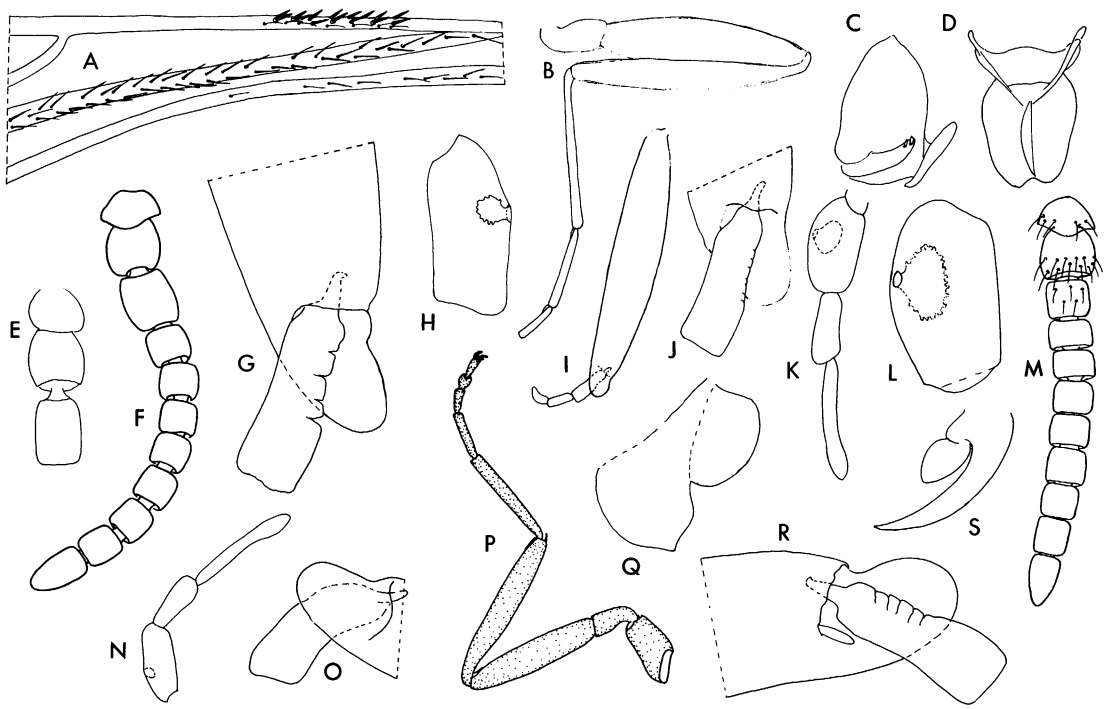

Fig. 84. *Gigantodax shannoni.* **A.** Portion of forewing, with C, Sc, and R. B–J. Male. **B.** Foreleg. **C.** Basimere and distimere. **D.** Ventral plate. **E.** Base of antenna. **F.** Antenna, different specimen. **G.** Calcipala and second tarsal segment. **H.** Second article of maxillary palp with sensory vesicle. **I.** Hind basitarsus with second to fourth tarsal segments. **J.** Calcipala and second tarsal segment. **K.** Maxillary palp of female. **L.** Second segment of posterior tarsus, with sensory vesicle. **M.** Antenna of female. **N.** Maxillary palp of male. **O.** Calcipala of male, with second tarsal segment. **P.** Foreleg of female. **Q.** Cercus and paraproct. **R.** Calcipala of female and second tarsal segment. **S.** Female claw.

otized, third antennal segment elongated, and dark irregular bands on the hypostomial bridge.

Gigantodax shannoni (Edwards)
Figures 84A–S, 85A–J, 86A–G

Simulium (*Gigantodax*) *shannoni* Edwards, 1931: 202. Orfila, 1936: 1528. Vargas, 1945: 197. Vulcano, 1967: 5.

Gigantodax shannoni: Wygodzinsky, 1961a: 460; 1961b: 563. Vulcano, 1967: 4; 1977: 290.

DIAGNOSIS: Yellow-orange medium-size species, with R_1 generally without spinules, gill branches 12 and 15 longer than remaining, frontoclypeus and thorax with obsolescent or absent platelets, and elongated terminal sensilla on larval antenna.

REDESCRIPTION: *Female.* Length of wing 4.2–4.8 mm. Head dark gray with reddish tinge; hairs golden yellow. Antenna yellowish brown; segments of flagellum with dense grayish pilosity. Maxillary palp dark brown. Scutum orange-yellow; pronotal sclerites whitish. Scutellum and metanotum as scutum. Pleural region as in scutum, with faint whitish pollinosity. Thoracic setae golden yellow. Halter whitish. Legs and abdominal setae golden yellow. Abdomen yellowish white; disc of tergites white.

Frontal angle 50°. Fronto-ocular triangle higher than wide. Shape and proportions of antennal segments as illustrated (fig. 84M). Mandibles with 24 teeth only on inner margin. Maxilla with about 34 teeth. Last segment of maxillary palp almost twice as long as penultimate (fig. 84K). Second segment of maxillary palp very short and stout, suboval, ratio length/width = 1:0.63. Sensory vesicle

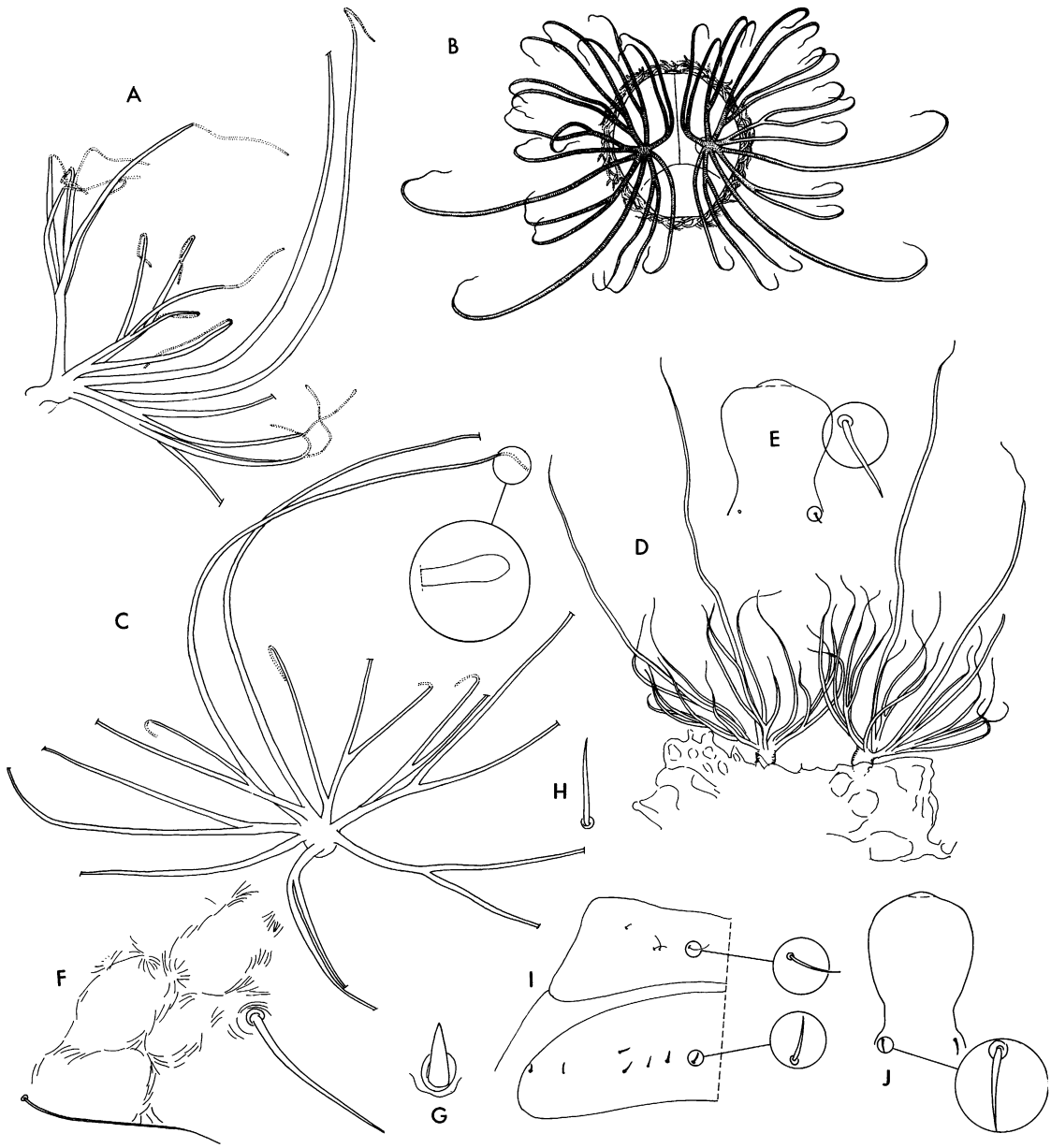

Fig. 85. *G. shannoni.* Pupa. **A.** Gill. **B.** Anterior portion of body with gills, frontal view. **C.** Gill. **D.** Anterior portion of body covered by cocoon, with gills, dorsal view. **E.** Frontoclypeus of female. **F.** Portion of thorax with trichomes and obsolescent reticulation. **G.** Hook of tergite IV. **H.** Anterodorsal trichome of tergite IV. **I.** Chaetotaxy of tergites I and II. **J.** Frontoclypeus of male.

large, with short but distinct neck (fig. 84L). Sc with 34–37 hairs. R and R_1 with setae in two or three irregular rows; spinules generally absent, occasionally a single spinule present. R_s with setae in one or two rows on distal two-thirds of upper and on basal third on undersurface, and in three irregular rows on distal two-thirds of undersurface (fig. 84A). A_1 almost reaching wing margin. Shape and proportions of foreleg segments as in figure 84B. Hind basitarsus 7.1–7.5 times as long as wide. Calcipala covering more than half

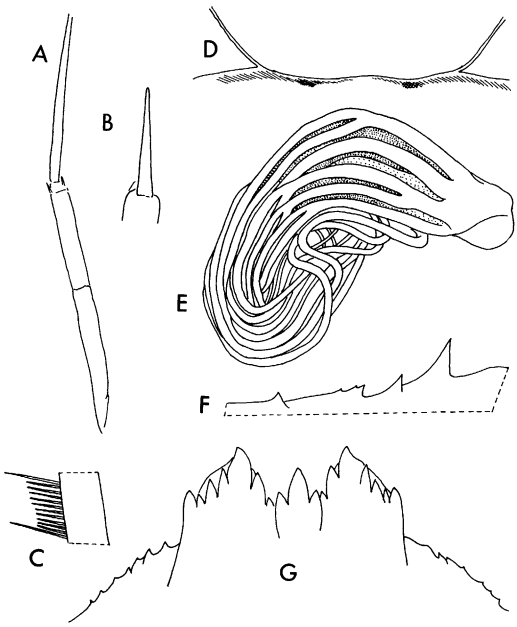

Fig. 86. *G. shannoni.* Larva. **A.** Antenna. **B.** Apical sensillum of antenna. **C.** Teeth of ray of cephalic fan. **D.** Cervical region. **E.** Gill histoblast. **F.** Mandibular serrations. **G.** Anterior portion of hypostomium.

the length of second tarsomere (fig. 84R). Basal tooth of claw as in figure 84S. Abdominal sterna with only delicate setae. Genitalia as usual for genus; cercus and paraproct as in figure 84Q.

Male. Length of wing 4.2–4.8 mm. Color as in female, but thorax from orange-yellow to orange, and abdomen tinged with light brown.

Holoptic. Shape and proportions of basal antennal segments shown in figure 84E, F; ratio length/width of first flagellomere 1:0.67–0.77. Last segment of maxillary palp twice as long as penultimate (fig. 84N). Sensory vesicle small (fig. 84H), subglobular, with distinct neck. Spinules on R_1 absent, as in female. Shape and proportions of some leg segments as in figure 84B, I. Fore basitarsus 14.0–14.1 times, hind basitarsus 5.5 times as long as wide. Calcipala surpassing middle of second tarsomere but falling considerably short of its apex (fig. 84G, J, O). Basimere much wider than long; distimere almost as long as basimere, with two apical spines (fig. 84C). Main body of ventral plate as long as wide (fig. 84D).

Pupa. Cocoon large, covering entire body of pupa except head and gills. Color of cocoon light brown, consisting of very delicate translucent fabric overlaid by meshwork of coarse, irregular threads, wih numerous apertures, especially on anterior portion of cocoon. Length of cocoon along midline dorsally 4.5–5.0 mm. Total length of body of pupa 4.0–4.5 mm; cephalopterothecal length 2.5–2.7 mm. Gills light brown, with 18 branches slender. Basal trunk of gills very short, as long as wide. Branches arranged in a radiating pattern, diverging from each other, basal portion subperpendicular to longitudinal axis of pupal body, progressively curved with their apical portions forwardly pointing (fig. 85A–D). All branches with thin and short apical respiratory filament, lost in many preserved specimens. Branches single or arising in pairs from common trunks, of varied length. Dorsomedian branches (1 and 2) arising from short trunk; dorsal branches (3 and 4) arising from elongate trunk; dorsolateral branches (5–8) arising from short basal trunk forming two secondary trunks each bearing two terminal branches; lateral branches (9–11) with short basal trunk giving off branch 11 and common trunk of branches 9 and 10. Branches 12 and 15 single, much longer than remaining (fig. 85B). Branches 13 and 14 and 16 and 17 each arising in pairs from short common trunk; branch 18 single. Surface of branches appearing minutely dotted, smaller dots forming annuli, large dots irregularly arranged. Shape and proportions of frontoclypeus of female and male as illustrated (fig. 85E, J); platelets absent. Facial trichomes spinelike. Platelets of thorax obsolescent. Thorax with three spinelike dorsocentral setae dorsocentral and two or three very fine hairlike setae (fig. 85F), their length 40–50 μm. Setae of tergite II slightly stronger (fig. 85I), length 40–42 μm. Tergites III and IV each with 1 + 1 short hooks (fig. 85G); anterodorsal setae (fig. 85H) as long or longer than hooks. Setae of tergites V–VIII continuous, consisting on tergite VII of 20–23 spines, length 28–39 μm, viz., slightly longer than setae of this segment. Specialized setae of eighth and ninth seg-

ments simple. Sternite IV with short hooked setae. Sternite V with 3 + 3 sternal plates, VI with 2 + 2, and VII with 1 + 1 hooks, one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 8.0 mm; width of head capsule 0.75 mm. Body shape as usual for genus; ventral papillae well developed. Body light colored, with very faint hypodermal pigment. Head light yellow. Spots of cephalic apotome faint. Hypostomial bridge lacking pattern elements. Antenna as long as stem of cephalic fan, with very faint pigment, third segment not perceptibly darker than preceding. Shape of antenna as in figure 86A; ratio of segments I–III = 1:0.68:1.1. Terminal sensillum (fig. 86B) elongate, 6.5 times as long as wide at base. Cephalic fan with about 30 rays, their teeth as in figure 86C, small teeth subequal in size. Mandibles with nine inner teeth and six or seven marginal serrations (fig. 86F). Maxillary palp 2.5 times as long as wide at base. Hypostomium (fig. 86G) with median tooth considerably short of level of corner tooth apex, reaching level of third intermediate tooth apex. Lines connecting apices of fourth lateral and corner teeth forming angle of approximately 100°. Hypostomium with six or seven lateral serrations and three or four hypostomial setae on each side. Cervical sclerites as in figure 86D. Histoblast brown, its shape as in figure 86E; characterized by very elongate anterior basal trunk. Perianal scales of medium size, forming complete circumanal ring. Recurrent struts only faintly pigmented. Crochet rings with about 95 rows of 22–24 hooks each.

MATERIAL EXAMINED: CHILE: *Llanquihue:* Casa Pangue, Dec. 1926 (R. and E. Shannon; CNC), 1 female. *Malleco:* Pehuenco, 1150 m, Dec. 13–17, 1963 (L. Pena; CNC), 1 female; Sierra de Nahuelbuta, W of Angol, 1200 m, Jan. 3, 1951 (E. Ross and Michelbacher; CAS), 1 female. *Nuble:* Las Cabras, Volcan Chillan, 1200 m, Dec. 10–23, 1954 (L. Pena; CNC), 1 male. *Talca:* Altos de Vilches, 1200 m, Oct. 5–7, 1972 (S. Coscarón, L. Pena, P. Wygodzinsky; AMNH), 1 male, 2 females (reared, and with their associated pupal exuviae), pupae, and larvae. *Curico:* El Coigual, Jan. 20–24, 1964 (L. Pena; CNC), 3 males, 11 females. *Santiago:* El Alfalfal, Los Maitenes, 1300 m, Oct. 10, 1972 (L. Pena, P. Wygodzinsky; AMNH), 1 male (reared, and with associated pupal exuviae).

DISTRIBUTION: Southern Argentina, southern and central Chile. The species was described from southern Neuquen and northern Rio Negro provinces in Argentina, and had not been reported elsewhere. The Chilean records given above extend the range of the species toward the west and especially the north.

DISCUSSION: We have examined the holotype and two paratypes, all from the collections of the British Museum; our adult specimens agree well with the types. The antennal flagellum of the types, described originally as "wholly blackish," is in reality yellowish brown, with considerable grayish pilosity, just as in our specimens.

The only other species of *Gigantodax* with an overall light color, including all wing setae, is *rufescens.* The adults can be distinguished easily by the different length of the calcipala in both sexes, extending well beyond the middle of the second tarsomere in *shannoni,* and not covering more than one-third of the tarsomere in *rufescens.* The larvae and pupae of the two species are completely different, as a comparison of the redescriptions easily shows. The pupa of *shannoni* is here described for the first time; its gills are peculiar, with their 18 slender branches provided with apical respiratory filaments and branches 12 and 15 being much longer than the remaining. This condition is much like that found in the species where branches 12 and 16 surpass the others in length; comparable conditions are not found in any other Chilean Patagonian species. Apical deciduous filaments are also found in other higher *Gigantodax.* The larva is characterized by the feeble pigment of the recurrent struts of the anal sclerite, a character it shares with the very similar larva of *G. gracilis* from which it can be distinguished as shown in our key. The larva of *G. dryadicaudicis* also shows weakly pigmented recurrent struts, but it is otherwise extremely different (see under heading of *dryadicaudicis*). Another apomorphy of the *shannoni* larva is the elongate terminal sensillum of the antenna. These specialized characters make it difficult to include *shannoni* in the *brophyi*

group, and we prefer to put it in a *cilicinus* subgroup.

Gigantodax destitutus, new species
Figures 87A–W, 88A–P

DIAGNOSIS: *G. destitutus* differs from related species by the pupal gill branches being moderately thickened basally and with the 12th and 16th branches longer than the others. The presence of only 2 + 2 hooks on abdominal sternite V of the pupa instead of 3 + 3 is also diagnostic.

DESCRIPTION: *Female.* Length of wing 3.3 mm. Head gray; clypeus brownish, pilosity brass colored. Antenna and maxillary palp light brown; scapus, pedicellus, and extreme base of first flagellomere orange colored, not conspicuously contrasting with rest of flagellum. Scutum light yellowish orange; scutellum and metanotum light yellowish brown. Pleuron light orange brown. Setae of thorax golden colored. Wings translucent; veins light brown. R-m conspicuously darkened. Setae of stem vein brown, with some golden colored ones on apical portion of patch, remaining setae of wing veins light brown. Halter very light brown, capitulum whitish. Legs light golden brown; setae golden yellow. First two or three abdominal tergites golden brown, the remaining dark brown, with their hind margins ivory colored, and disc extensively lightened. Abdominal hairs golden colored.

Frontal angle 45°. Fronto-ocular triangle about as high as wide (fig. 87B). Shape and proportions of antennal segments as shown in figure 87A. Mandible with number of teeth unusually small (17–18), rapidly diminishing in size from large apical ones on. Maxilla with 19–20 teeth. Second segment of maxillary palp (fig. 87K) oval, ratio length/width = 1:0.5. Sensory vesicle (fig. 87L) medium size, with distinct neck. Sc with 19–20 hairs. R with setae in two or three irregular rows; setae very numerous at "nodus." Setae on R_1 in one, rarely in two irregular rows, interspersed with rather slender spinules, beginning slightly basal to insertion of Sc on C; spinules about as numerous as interspersed setae. R_s with row of setae on apical half of upper and two rows on undersurface of vein. A_1 terminating well before wing margin. Shape and proportions of fore and hind leg segments as in figure 87C, E. Hind basitarsus 7.0–7.2 times as long as wide. Calcipala almost reaching apex of second tarsomere (fig. 87O). Basal tooth of claws as in figure 87D. Abdominal sterna with only simple, delicate hairs. Eighth sternite and gonapophysis without special characters. Cercus (fig. 87M) unusually low; paraproct as illustrated. Genital fork as in figure 87P. Spermatheca normal.

Male. Length of wing 2.9–3.1 mm. Color as in female, but disc of abdominal tergites uniformly dark. Holoptic. Shape and proportions of antennal segments as in figure 87J; ratio length/width of first flagellomere 1:0.5. Last segment of maxillary palp very slightly longer than penultimate (fig. 87H). Sensory vesicle (fig. 87I) small, subglobose. Wing as in female; Sc with about 16 setae. Shape and proportions of leg segments as in figure 87G. Fore basitarsus 10–11 and hind basitarsus 5.65–5.9 times as long as wide. Calcipala almost reaching apex of second tarsomere (fig. 87N). Distimere over two-thirds as long as basimere, with two apical spines (fig. 87Q, S). Main body of ventral plate as long as wide (fig. 87T). Hooks and aedeagus as illustrated in figure 87Q, R.

Pupa. Cocoon of irregular shape, baglike, covering whole body except gills. Color of cocoon light brown; threads visible with low magnification, not tightly woven, forming distinct mesh leaving occasional small "windows." Length of cocoon approximately 3 mm. Total length of body of pupa 3.8–4.3 mm; cephalopterothecal length 2.0–2.2 mm. Gills light brown, with 18 terminal branches, originating from four strongly divergent primary branches (dorsal, dorsolateral, ventrolateral, and ventral) as follows (fig. 88A–C, E). Dorsal primary branch with first secondary branch arising very close to base, second to fourth arising at some distance from base, subcontiguous or not very distant from each other. Dorsolateral branch dividing shortly beyond its base into two secondary branches. Dorsoventral branch with two secondary branches, the first divided in two branches and the second divided into four terminal branches, subcontiguous or arising at different levels. Ventral primary branch similar in structure to dorsal primary branch. Most branches perpendicular to longitudinal axis of pupa, only terminal portions curved for-

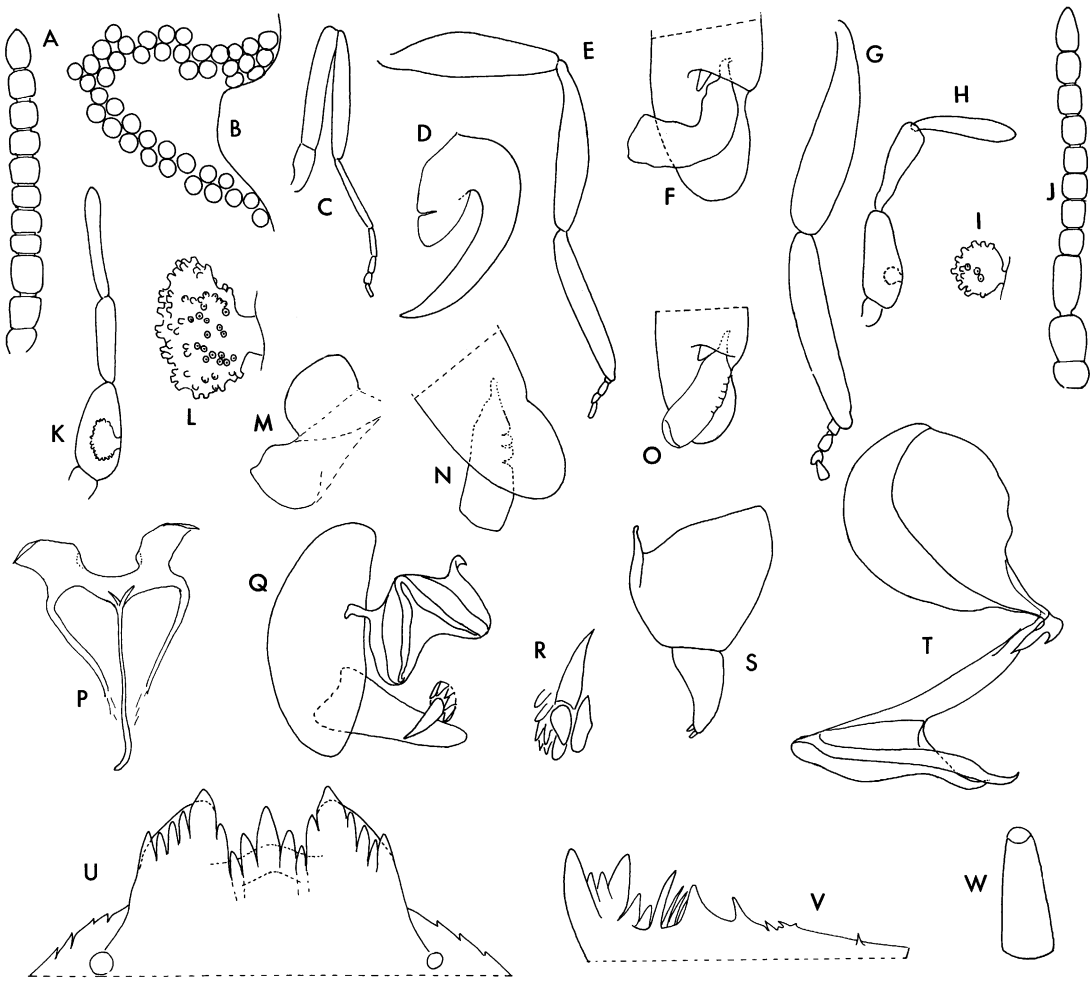

Fig. 87. *Gigantodax destitutus.* A–F. Female. **A.** Antenna. **B.** Fronto-ocular triangle. **C.** Foreleg. **D.** Claw. **E.** Posterior leg. **F.** Calcipala, with second tarsal segment. G–J. Male. **G.** Hind leg. **H.** Maxillary palp. **I.** Sensory vesicle of maxillary palp. **J.** Antenna. **K.** Maxillary palp of female. **L.** Sensory vesicle of maxillary palp of female. **M.** Cercus and paraproct. **N.** Calcipala, with second tarsal segment, male. **O.** Same, female. **P.** Genital fork. Q–T. Male genitalia. **Q.** Basimere and distimere, basal plate, and endoparameral organ. **R.** Endoparameral organ. **S.** Basimere and distimere. **T.** Ventral plate with median sclerite. U–W. Larva. **U.** Distal region of hypostomium. **V.** Apical portion of mandible. **W.** Maxillary palp.

ward. Individual terminal branches slender, tapering from thicker bases to filiform apical portion, the latter corresponding to respiratory filaments. Surface of branches minutely dotted, distribution of dots as in *G. basinflatus.* Shape and proportions of frontoclypeus of female and male pupa as in figure 88H, I; with numerous verrucose platelets (fig. 88L) similar to those of thorax. Facial trichomes elongate, very thin, hairlike. Thorax with platelets numerous, verrucose; arranged as in figure 88J, N. Chaetotaxy of thorax as in figure 88F. Dorsocentral and dorsolateral trichomes consisting of very delicate long hairs (fig. 88N, O). Setae of abdominal tergites I very short (18–20 μm) and delicate; setae of tergite II slightly thickened at base (fig. 88D), length 30–33 μm. Tergites III and IV each with 4 + 4 somewhat elongate hooks; anterodorsal setae very small (fig. 88P). Setae of

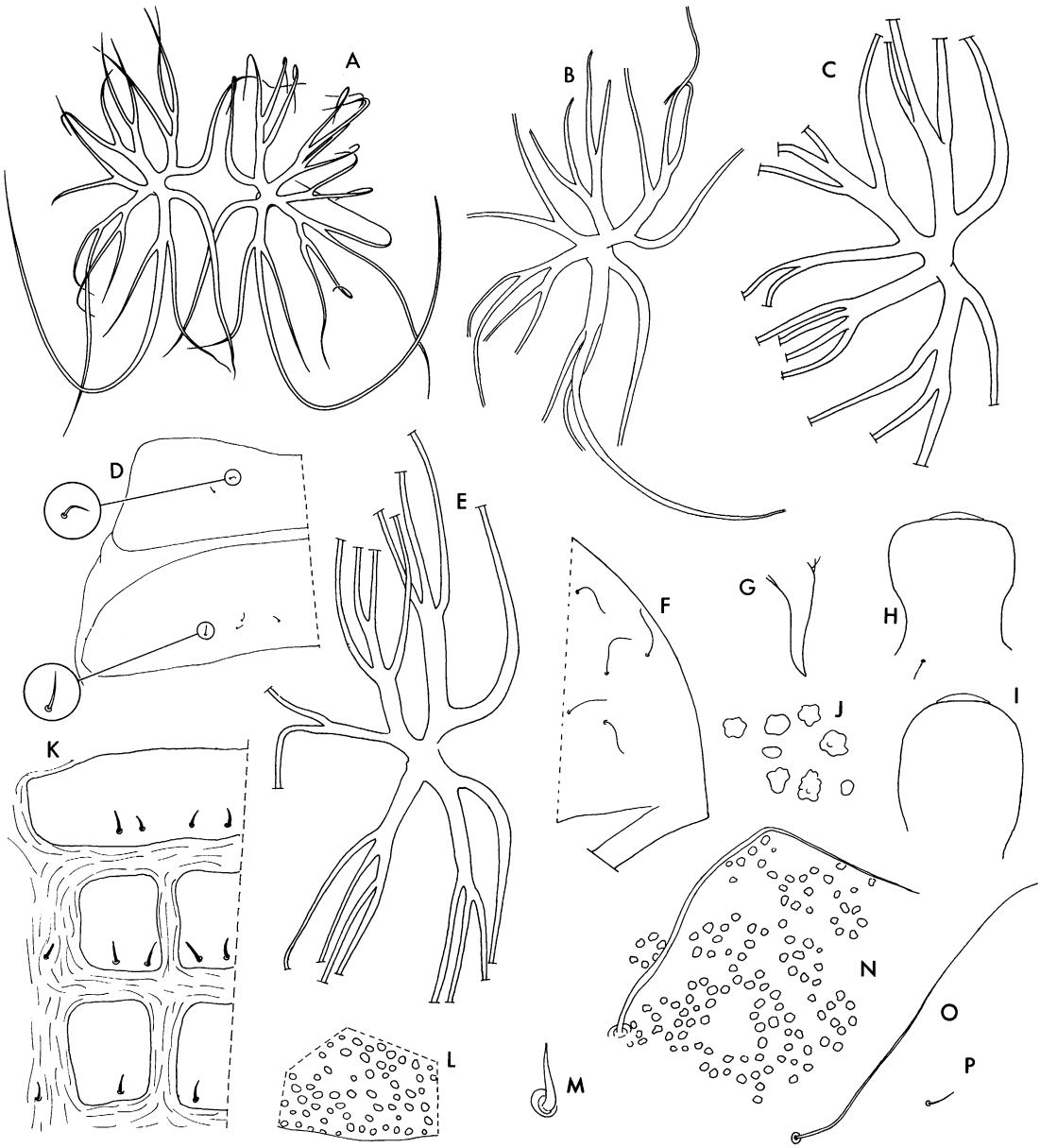

Fig. 88. *G. destitutus.* Pupa. **A.** Gills, front view. **B.** Gill. **C.** Basal portion of other gill. **D.** Chaetotaxy of abominal tergites I and II. **E.** Base of different gill. **F.** Portion of thorax, with trichomes. **G.** Terminal hook of abdomen. **H.** Frontoclypeus of female. **I.** Same, male. **J.** Platelets of clypeus. **K.** Chaetotaxy of sternites V–VII. **M.** Hook of tergite IV. **N.** Dorsocentral tricome of thorax, with platelets. **O.** Different dorsocentral trichome of thorax. **P.** Anterosublateral trichome of III tergite.

tergites V–VIII continuous, consisting on tergite VII of 33–40 spines, length 15–20 μm, viz., at least one-half as long as setae of this tergite. Specialized setae of segments VIII and IX simple, from straight to variously curved. Sternite IV with very small, inconspicuous setae; V and VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural mem-

brane of segments VI and VII (fig. 88K). Sternite VIII glabrous. Terminal hooks as shown in figure 88G.

Mature larva (description based on incomplete head capsule exuvium found in cocoon with pupa). Cephalic apotome brown, pattern elements fading into background. Hypostomial bridge lacking pattern elements. Antenna with third segment as long or longer than first and second combined. Mandible (only one examined) with seven inner teeth and seven marginal serrations (fig. 87V). Maxillary palp as shown in figure 87W. Hypostomium with median tooth considerably short of level of corner tooth apex, but post level of third intermediate tooth apex (fig. 87U). Line connecting apex of fourth lateral tooth and corner tooth intersecting at 105°. Hypostomium with six lateral serrations and three hypostomial setae in each row.

HOLOTYPE: COLOMBIA: *Cundinamarca:* 2 km SE of Alban, 2400 m, Aug. 24, 1969 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female, allotype, 2 males, 3 females, paratypes (all reared, and with their associated pupal exuviae; *ibid.,* Aug. 6, 1967 (P. and B. Wygodzinsky; AMNH), 2 males, 1 female, paratypes (all reared, and with associated pupal exuviae), pupae. VENEZUELA: *Merida:* road from Apartaderos to Santo Domingo, 3400 m, Feb. 16–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 male (reared, and with associated pupal exuviae), pupae.

ETYMOLOGY: The specific name is taken from the Latin *destitutus,* lacking, devoid of, an allusion to the reduced number of hooks on sternite V of the pupa.

BIOLOGY: The Colombian material of the species was collected at 2400 m, in a small stream in an open meadow with a water temperature of 16°C, together with several other species of *Gigantodax* (*cervicornis, septenarius, wygodzinskyi*) and of *Simulium* (*S. metallicum, S. paynei,* and others). The Venezuelan specimens were obtained at 3400 m, a much higher altitude, in a larger stream with a water temperature of 15°C, where such species as *Gigantodax impossibilis, cervicornis,* and *Simulium bicoloratum, S. cormonsi,* and *S. jaimeramirezi* also occurred.

DISCUSSION: The structure of the gills of the pupa is somewhat similar to that found in *basinflatus,* but the latter species has only 17 branches as opposed to 18 in *destitutus,* and, of course, the primary branches of the gill are conspicuously inflated in *basinflatus.* Among the differences between the two species are the color of the scutum of the adults, orange in *destitutus,* dark brown in *basinflatus.* The dorsocentral trichomes of the pupal thorax in *basinflatus* are in the shape of strong setae, as are the facial trichomes; in *destitutus,* these trichomes are in the shape of very fine hairs. The reduction of the hooks of sternite V of the pupal abdomen to 2 + 2, as found in *destitutus,* is a unique character, not shared by *basinflatus* or, to our knowledge, by any other *Gigantodax.*

The description of the species is based on Colombian material. The Venezuelan specimens are very similar, but the only male reared (no female was obtained), has a scutum which is dark orange instead of light orange as in Colombian specimens. This species, like *basinflatus,* often has the pupal gills inflated basally, which is even more developed in the other species of the *cilicinus* group.

Gigantodax basinflatus, new species

Figures 89A–Z, 90A–K, 91A–P

DIAGNOSIS: Characterized in the adult by the dark brown scutum in both sexes, and in the pupal stage by the basally inflated gills with 17 filaments.

DESCRIPTION: *Female.* Length of wing 3.9–4.1 mm. Head including clypeus piceous; pilosity brass colored. Mouthparts and antenna from dark brown to piceous; scapus, pedicellus, and extreme base of first flagellomere dark orange colored. Scutum dark brown, with faint light colored median longitudinal line. Scutellum very slightly lighter than scutum, metanotum as dark as scutum. Pleural region dark brown, faintly tinged with violaceous. Short pilosity of thorax brass colored, long setae on posterior portion of scutum and on scutellum dark brown. Wing slightly fumose; veins brown. Setae on stem vein dark brown, remaining setae light brown. Halter very light brown, capitulum ivory colored. Legs light brown; setae concolorous. Abdominal ter-

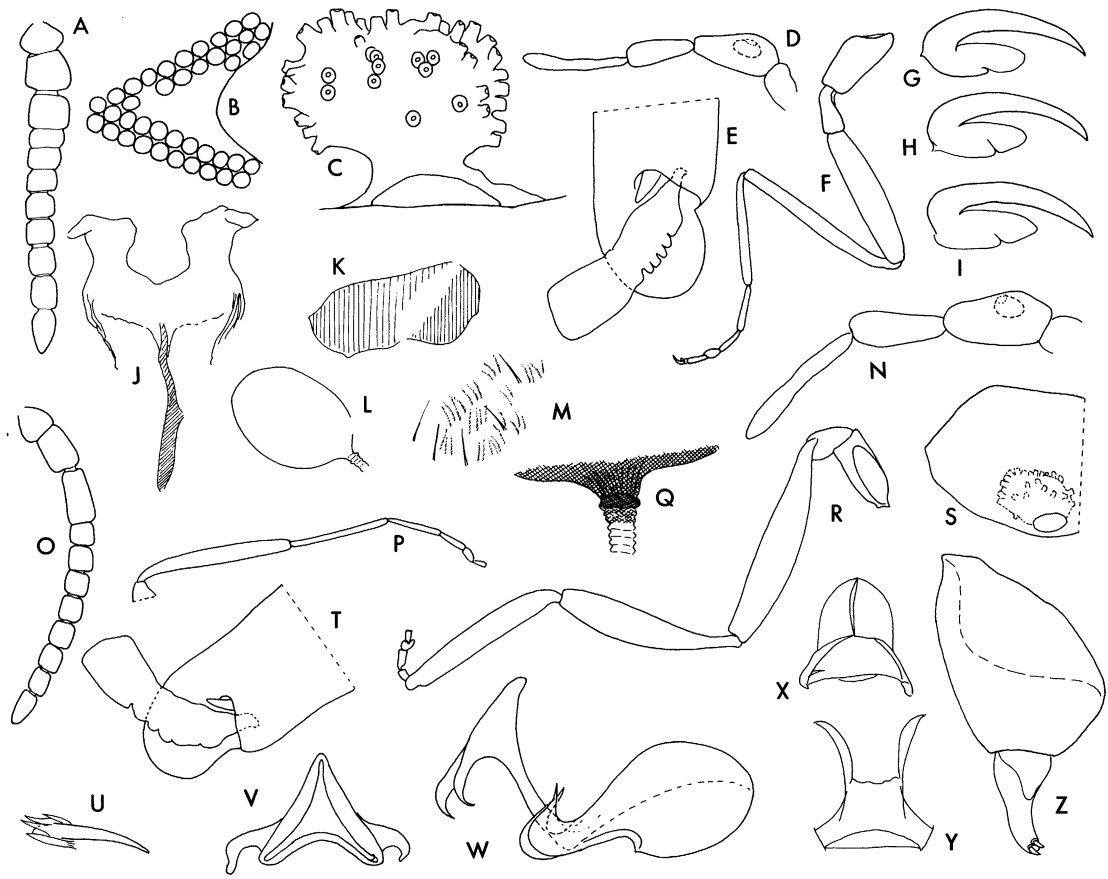

Fig. 89. *Gigantodax basinflatus.* A–M. Female. **A.** Antenna. **B.** Fronto-ocular triangle. **C.** Sensory vesicle of maxillary palp. **D.** Maxillary palp. **E.** Calcipala. **F.** Foreleg. **G–I.** Claw. **J.** Genital fork. **K.** Cercus and paraproct, schematic. **L.** Spermatheca. **M.** Microstructure of spermatheca wall. N–P, R–Z. Male. **N.** Maxillary palp. **O.** Antenna. **P.** Foreleg. **Q.** Base of spermatheca. **R.** Hind leg. **S.** Sensory vesicle of maxillary palp, in situ. **T.** Calcipala, with second tarsal segment. **U.** Endoparameral organ. **V.** Ventral plate. **W.** Ventral plate with median sclerite, side view. **X.** Ventral plate, full view. **Y.** Median sclerite. **Z.** Basimere and distimere.

gites brown, velvety, their hind margin not or almost imperceptibly lighter; in some specimens, tergites III–V slightly lighter on disc. Abdominal setae brass colored.

Frontal angle 55–60°. Fronto-ocular triangle about as long as wide (fig. 89B). Shape and proportion of antennal segments as in figure 89A. Mandible with 22–24 teeth. Maxilla with approximately 22 teeth. Distal segment of maxillary palp slightly less than twice as long as penultimate. Second segment of maxillary palp suboval, narrowed apically (fig. 89D), ratio length/width = 1:0.53–0.56. Sensory vesicle comparatively shorter, with distinct neck (fig. 89C); Sc with 30–32 hairs. R with setae in one or two irregular rows. R_1 with setae in one or two rows; spinules present, well developed, beginning at level of insertion of Sc on C, interspersed among hairs in one or two rows. R_s with setae in one row on apical portion of upper surface, in two irregular rows on undersurface of vein. A_1 almost reaching wing margin. Shape and proportions of foreleg segments as shown in figure 89F. Hind basitarsus 8.48–8.86 times as long as wide. Calcipala slightly past middle of second tarsomere (fig. 89E). Basal tooth of claws (fig. 89G–I) elongate, apex frequently

Fig. 90. *G. basinflatus.* **A, B.** Gill of pupa, ventral view. **C–E.** Some gill branches of pupa, with caducous apical filament in E. **F.** Hook on tergite IV. **G.** Anterosublateral chaeta of abdominal tergite III. **H.** Chaetotaxy of abdominal tergites I–II. **I.** Trichome of thorax and platelets. **J.** Specialized setae of terminal segments of abdomen. **K.** Portion of thorax, with trichomes.

appearing rounded. Abdominal sterna with only delicate hairs. Eighth sternite and gonapophyses without special characters. Cercus and paraproct as in figure 89K; genital fork as in figure 89J. Spermatheca (fig. 89L) oval, sclerotization extending to neck of spermathecal duct, then abruptly terminated (fig. 89Q); inner surface of spermatheca delicately rugose and with scattered spicules (fig. 89M).

Male. Length of wing 3.6–3.9 mm. Color much as in female, but in some specimens posterior three or four abdominal tergites lightened on disc.

Holoptic. Shape and proportions of antennal segments as in figure 89O. Ratio length/width of first flagellomere 1:0.48. Last segment of maxillary palp 1½ times as long as penultimate (fig. 89N). Sensory vesicle (fig. 89S) slightly oval, comparatively large. Wing much as in female, but Sc with only 20–22 hairs, and setae on R in a single row. Shape and proportions of part of fore and hind leg

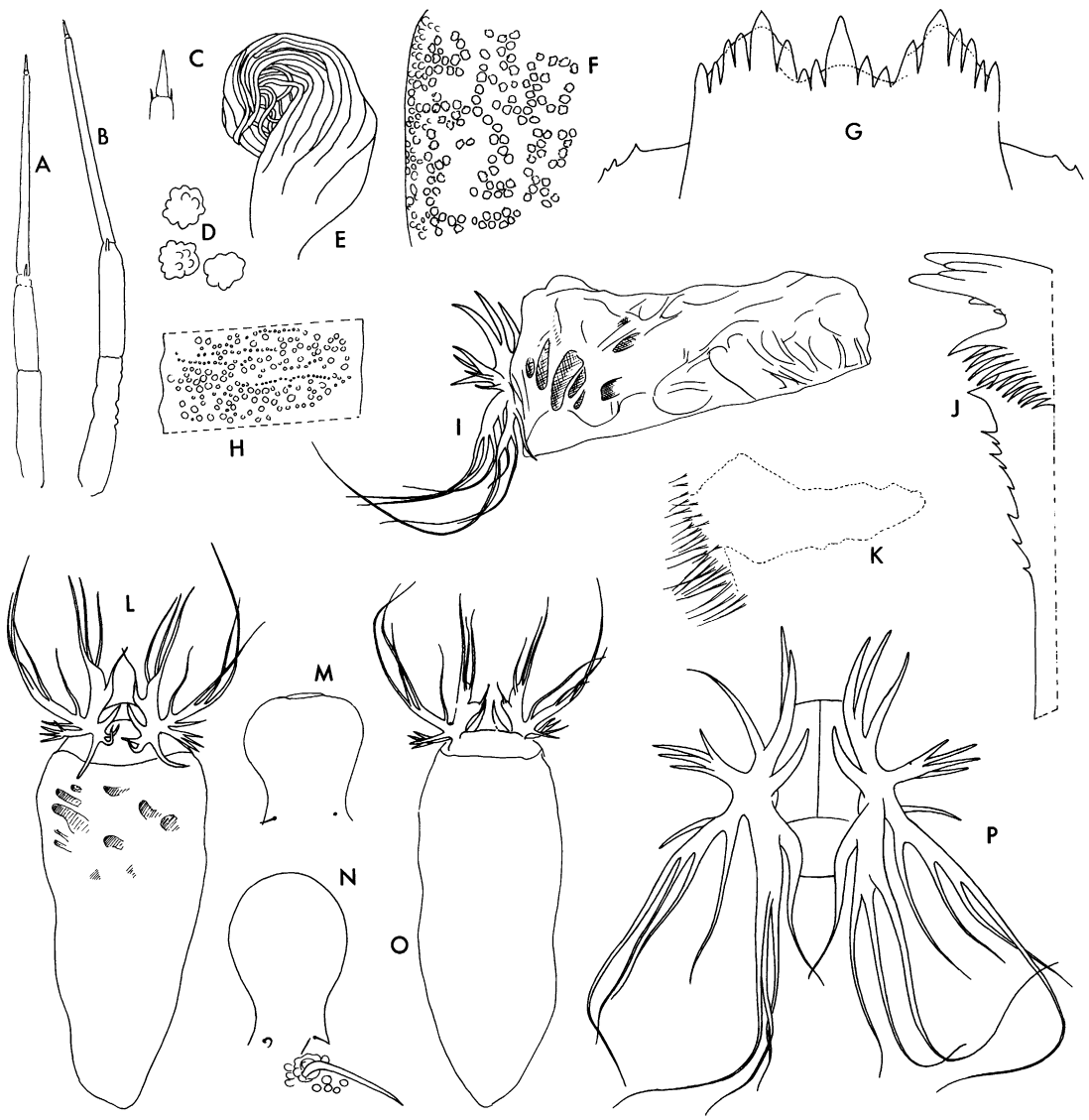

Fig. 91. *G. basinflatus.* **A, B.** Antennae of larva. **C.** Apical sensillum of antenna. **D.** Platelets of frontoclypeus. **E.** Gill histoblast. **F.** Portion of frontoclypeus with platelets. **G.** Anterior portion of hypostomium. **H.** Microstructure of distal portion of gill branch. **I.** Pupa in cocoon, side view. **J.** Apex of mandible. **K.** Lateral sclerite of proleg. **L.** Pupa in cocoon, dorsal view. **M.** Frontoclypeus of female. **N.** Frontoclypeus of male. **O.** Pupa in cocoon, ventral view. **P.** Head and gills, frontal view.

segments as in figure 89P, R. Fore basitarsus 12.0 times, hind basitarsus 7.3–7.7 times as long as wide. Calcipala slightly past middle of second tarsomere (fig. 89T). Genitalia as in figures 89U–Z. Distimere about two-thirds as long as basimere, with two apical spines. Main body of ventral plate as long as wide.

Pupa. Cocoon large, covering entire body except head and gills (fig. 91I, L, O). Color of cocoon light brown; loosely woven, threads combined into ropelike structures forming irregular mesh over body of pupa, with many "windows," especially on anterior portion of body. Anterior border of cocoon not well defined. Length of cocoon along dorsum 3.0–4.5 mm. Total length of body of pupa ap-

proximately 3.5 mm; cephalopterothecal length 2.2–2.3 mm. Gill (figs. 90A–E, 91I, L, O, P) light brown, their surface appearing polished; each gill with 17 secondary branches inserted on four primary branches (dorsal, dorsolateral, ventrolateral, and ventral) (fig. 91P). Primary branches and basal portions of secondary branches variously thickened, perpendicular to longitudinal axis of body, apical portion of secondary branches directed forward. Dorsal primary branch with four short secondary branches, two subbasal, and two subapical. Dorsolateral branch also with four even shorter secondary branches, their bases subcontiguous. Ventrolateral branch with one long secondary branch arising directly from its base, the points of insertion of the four remaining secondary branches staggered or subcontiguous. Ventral primary branch thickest, with four long secondary branches arranged as in foregoing branch. Primary branches conspicuously swollen. Secondary branches slender, gradually tapering distally, apical portion extended into respiratory filament, longest on lateroventral and ventral branches. Surface of branches minutely pitted, pits of conspicuously different sizes, the smaller ones forming irregular spiral structure (fig. 91H). Shape and proportions of frontoclypeus of female and male as in figure 91M, N; with numerous verrucose platelets (fig. 91D) arranged in peculiar groups (fig. 91F). Facial trichomes in form of stout setae. Thorax with platelets (fig. 90I) similar to those of frontoclypeus. Three dorsocentral trichomes in shape of strong setae but one much more slender than the remaining; two or three dorsolaterals in shape of fine hairs (fig. 90K). Setae of abdominal tergite I slender, length 55–80 μm, those of tergite II very similar though thicker and somewhat shorter (50–60 μm) (fig. 90H). Tergites III and IV each with 4 + 4 short hooks (fig. 90F). Anterosublateral seta stout (fig. 90G). Setae of tergites V–VIII slender, length on segment VII 37–50 mm. Spine combs on tergites VI–VIII continuous or rarely interrupted, consisting on tergite VII of 16–23 spines, length 20–22 μm, viz., about half as long as setae of this segment. Specialized setae of segments VIII and IX simple, straight, or variously bent or branched (fig. 90J). Sternite IV with setae or hooks or both, single or arranged in pairs; sternite V with 3 + 3, VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Small for the genus, length 6.5–7.0 mm; width of head capsule approximately 0.7 mm. Body shape as usual for the genus; ventral papillae small but distinct. Color of larva brownish due to rather intense overall hypodermal pigment. Head from light to dark brown, pattern elements of cephalic apotome not conspicuous, blending into brown background. Hypostomial bridge of general color, faintly lighter longitudinally along middle. Antenna as long as, or slightly shorter than, stem of cephalic fan, faintly pigmented; third segment darkest. Shape of antennae as in figure 91A, B; ratio of segments I–III = 1:0.57–0.68:1.43–1.67. Terminal sensillum approximately four times as long as wide at base (fig. 91C). Cephalic fans with 31–35 rays. Mandible (fig. 91J) with 8–11 inner teeth and 8–9 marginal serrations. Maxillary palp approximately 2.7 times as long as wide. Hypostomium as in figure 91G. Median tooth long, almost reaching level of corner tooth apex. Line connecting apices of fourth lateral tooth and corner tooth intersecting at angle of approximately 100°. Hypostomium with six or seven lateral teeth and five or six hypostomial setae in each row. Cervical sclerites as in *G. cormonsi.* Histoblast as in figure 91E, brown in fully mature specimens. Lateral sclerite of proleg as figure 91K. Perianal scales well developed, forming complete circumanal ring. Recurrent struts of anal armature distinct, but becoming obsolescent toward lower arms of anal sclerite. Crochet ring with 103–108 rows of 19–21 hooks.

HOLOTYPE: COLOMBIA: *Cundinamarca:* Paramo de Chisaca (or Sumapaz), 3700 m, Aug. 28, 1969 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES: Same data as holotype (AMNH), female (allotype), 4 males and 16 females (all reared, and with their associated pupal exuviae), pupae, and larvae. Additional specimens: Same locality as holotype, June 30, 1965, and July 2, 1965 (P. and B. Wygodzinsky; AMNH), pupae and larvae; road Bogota-Choachi, 3250 m, July 13 and 19, 1967 (P. and B. Wygodzinsky; AMNH), lar-

vae; ibid., 3300 m, July 13, 1967 (P. and B. Wygodzinsky; AMNH), one pupa, larvae; Paramo de Guasca, 3300 m, Aug. 4, 1969 (P. and B. Wygodzinsky, E. Schmidt-Mumm; AMNH), one pupa. ECUADOR: *Pichincha:* road Quito-Papallacta, W of Papallacta, 3900 m, July 24, 1969 (P. and B. Wygodzinsky; AMNH), two pupae; road Quito-Papallacta, San Juan, Paramo de Guamani, 3700 m, Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), one pupa.

ETYMOLOGY: The specific name is taken from the Latin *basis,* pedestal, support, and *inflatus,* inflated, in reference to the structure of the gills of the pupa.

BIOLOGY: This is a high-altitude species. The aquatic instars of *basinflatus* are most common at considerable altitudes, generally between 3300 and 3900 m, in the paramos. They occur in very small clear watercourses, of temperatures between 4 and 9°C; water running in shallow roadside ditches was a frequent habitat where large numbers of specimens could be collected. Watercourses where the species was observed were generally unshaded. Larvae and pupae were in most cases found attached to grasses and other trailing vegetation, though pupae were also located on the underside of stones resting on the bottom of the streams which did not surpass a width of 20 cm and a depth of 5 cm.

DISCUSSION: The most striking characters of this species are found in the structure of the gill of the pupa and of the spermatheca; in the former, the conspicuously swollen basal branches, and in the latter the extension of the sclerotization to the neck of the spermathecal duct. The elongated basal tooth of the female claw is also peculiar. In the Ecuadorian specimens the basal portion of the pupal gills is slightly less inflated than in Colombian material.

Gigantodax mariobordai, new species

Figures 92A–J

DIAGNOSIS: Characterized by pupal gills with 17 branches, thickened basally, some of them directed forward.

DESCRIPTION: Based on the remains of several pupae, found adhered to stones.

Female and male unknown, only the remains of calcipala (fig. 92J) and female claws, the latter with subtriangular subbasal tooth as in figure 92D.

Pupa. Gills with 17 arborescent branches, arising from a basal stem (figures 92A–C, F, H). Gill branches stout at base, tapering from base to apex, semirigid; surface of branches uniformly dotted, with small incisures. Some gill branches rounded apically (because apex lost in some filaments, presence of respiratory filament questionable; fig. 92I). Thorax with small platelets. Trichomes of thorax elongate (fig. 92G). Chaetotaxy of abdomen typical for the genus. Setae of abdominal tergites I–II as shown in figure 92E. Apex of abdomen with looped or spiraled setae; distal abdominal hooks well developed.

Larva. Unknown.

BIOLOGY: Pupal remains were found adhering to stones in a small creek with clear, cold water. One pupa of *Simulium* (*Hemicnetha*) *huairayacu* Wygodzinsky and larvae of *Simulium* (*Pternaspatha*) sp. were collected at the same locality.

HOLOTYPE: BOLIVIA: *La Paz:* road from La Paz to La Cumbre about 4000 m, Oct. 27, 1968 (S. Coscarón; MLP), pupa.

PARATYPES (AMNH): Same data as holotype, pupae.

ETYMOLOGY: Named for Dr. Mario Borda, from University San Simon, Cochabamba, Bolivia, who helped very much with the second author's travels in that country.

DISCUSSION: This species was collected probably in the typical habitat of *G. bolivianus* (Quebrada de Cillunticara, a locality not found on maps, but at the same altitude). *Gigantodax mariobordai* has the female claw with a subtriangular subbasal tooth, and in *bolivianus,* it is hook shaped and proportionally larger.

G. pennipunctus from Cuzco, Peru, has very similar gills, but with 18 branches, transverse wrinkles, small cuticular projections, and apically with caducous respiratory filaments on the apices.

According to the morphology of pupal gills only, the most closely related species is *incomitatus*: both have the gill branches minutely and uniformly dotted, and some branches are apically rounded. We cannot say if *mariobordai* also has respiratory filaments apically, because most apical portions are missing. Because imagos and larvae are unknown, it is very difficult to decide in which species group *mariobordai* should be included. As the gill branches resemble *pennipunc-*

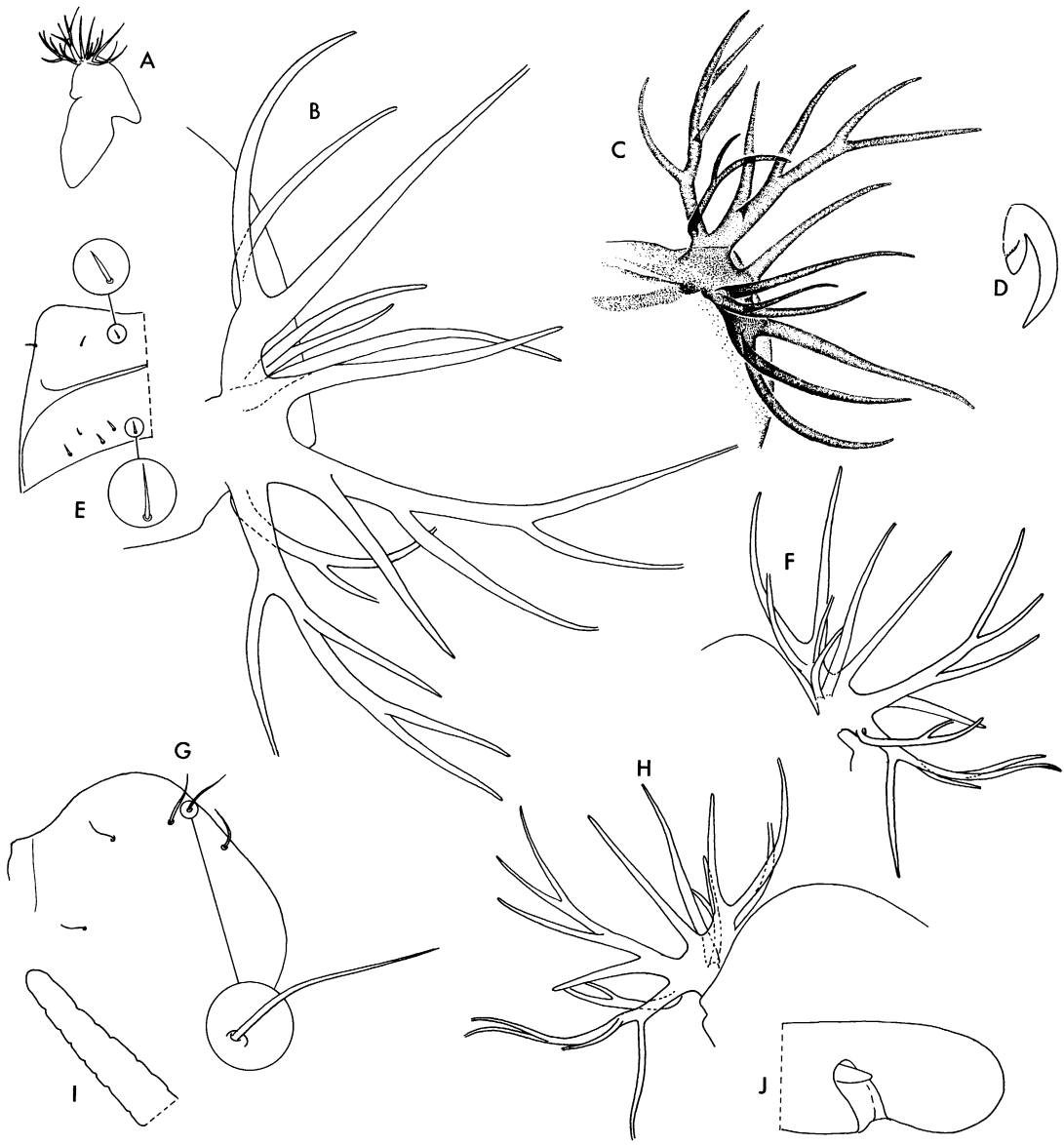

Fig. 92. *Gigantodax mariobordai.* **A.** Thorax with gill. **B.** Left gill, mesad. **C.** Right gill. **D.** Claw of female. **E.** Chaetotaxy of abdominal tergites I and II. **F.** Gill, different specimen. **G.** Thorax, with trichomes. **H.** Gill. **I.** Apex of gill branch. **J.** Calcipala.

tus, we tentatively place this species in the *cilicinus* group, awaiting further information.

Gigantodax incomitatus, new species
Figure 93A–U

DIAGNOSIS: This species is characterized by the pupal gill with 10–11 branches, strongly diverging perpendicular to the longitudinal axis of the pupal body and distally bent caudad.

DESCRIPTION: Female unknown.

Male (pharate). Rather small (wing length less than 4.0 mm). Scutum in alcohol light orange, but dark reddish brown when dried. Holoptic. Shape and proportions of antennal segments as in figure 93A; ratio length/width of first flagellomere 1:0.67–0.71. Distal seg-

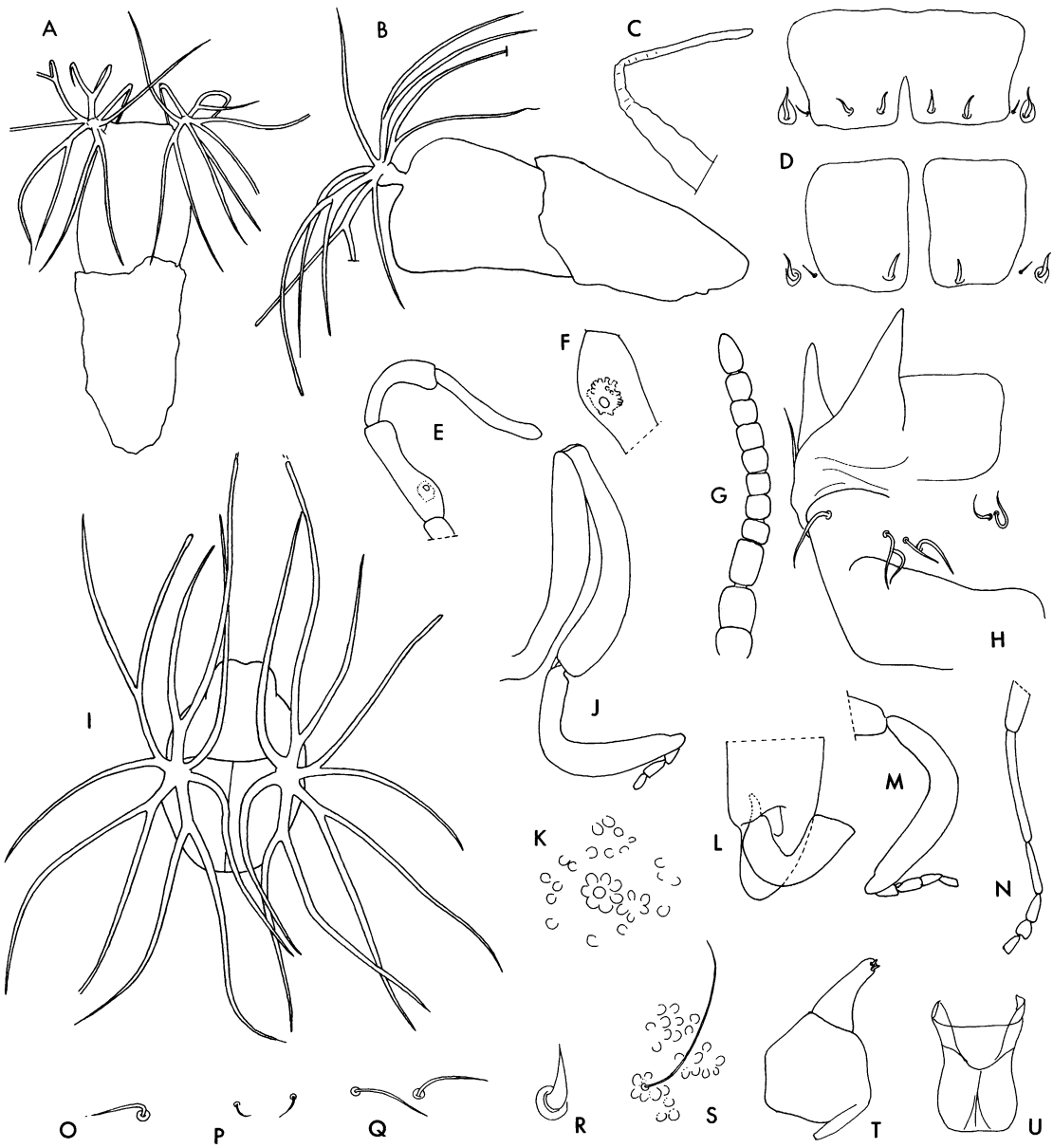

Fig. 93. *Gigantodax incomitatus.* A–D. Pupa in cocoon. **A.** Dorsal view. **B.** Same, side view. **C.** Apex of gill branch, with base of respiratory filament. **D.** Sternites VI and VII. E–G. Male. **E.** Maxillary palp. **F.** Portion of second article of maxillary palp, with sensory vesicle. **G.** Antenna. **H.** Distal portion of abdomen, with modified setae and terminal spines. **I.** Anterior portion of body of pupa, with gills, frontal view. **J.** Hind leg of male. **K.** Platelets of thorax. **L.** Calcipala, with second tarsal segment. **M.** Posterior tarsus of male. **N.** Fore tarsites of male. O–S. Male pupa. **O.** Anterosublateral trichome of abdominal tergite III. **P.** Setae of abdominal tergite I. **Q.** Setae of abdominal tergite II. **R.** Hook of tergite IV. **S.** Trichome of thorax. **T.** Basimere and distimere. **U.** Ventral plate.

ment of maxillary palp slightly longer than penultimate (fig. 93E). Sensory vesicle small, subglobular (fig. 93F). Length of wing not known (probably less than 4 mm). Setae on R in one row. R_1 with well-developed spinules, as or more numerous than interspersed setae. Fore tarsomeres as in figure 93N, hind legs as in figure 93J; calcipala slightly past

center of second tarsomere (fig. 93L). Distimere over two-thirds as long as basimere (fig. 93T), with two apical spines. Main body of ventral plate about as long as wide (fig. 93U).

Pupa. Cocoon small, reduced to a short sleeve covering abdomen (fig. 93A, B). Thorax, head, and gills fully exposed; cocoon tightly woven. Length of cocoon along dorsum 3 mm. Length of body of pupa 4.1 mm, cephalopterothecal length 2.5 mm. Gill light colored, with very short basal trunk, with 10 terminal branches on one gill, and 11 on other (fig. 93A, B, I). Dorsal (first) and ventral (last) branches single, directly inserted on trunk of gill; remaining eight or nine branches arising in pairs from short primary branches. All branches strongly diverging, situated on a plane roughly perpendicular to longitudinal axis of body of pupa; apical portions of branches bent caudad (fig. 93A, B). Branches slender but semirigid, not filamentous, tapering from base to apex; second and fourth branches, as counted from below, rounded apically, the remaining pointed apically with very short respiratory filament easily detached (fig. 93C). Surface of branches minutely and uniformly dotted; cuticular projections absent. Frontoclypeus not examined in detail, with numerous smooth platelets; facial trichomes not examined. Thorax with smooth platelets (fig. 93K, S), many with faint outlines only. Dorsocentral trichomes not examined; dorsolateral trichomes (fig. 93S) very delicate, hairlike. Setae of abdominal tergite I minute (fig. 93Q), length 3–4 μm; setae of tergite II much larger, length 15–25 μm (fig. 93P). Tergites III and IV each with 4 + 4 short but narrowly pointed hooks (fig. 93R); anterodorsal setae strong (fig. 93O), about as long as hook. Setae of tergites V–VIII slender, their length on tergite VII 55–60 μm. Spinecombs on tergites VI–VIII entire or shortly interrupted, consisting on tergite VII of about 24 spines, length 10–12 μm, viz., about one-fifth length of the setae of this segment. Specialized setae of segments VIII and IX (fig. 93H) simple, curved, but not branched. Sternite IV with four strong, spinelike setae: V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII (fig. 93D). Sternite VIII glabrous. Terminal hooks of abdomen stout (fig. 93H).

Larva. Unknown.

HOLOTYPE: VENEZUELA: *Merida:* road from Apartaderos to Santo Domingo, 3400 m, Feb. 16–28, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 pupa with pharate male.

ETYMOLOGY: The specific name is taken from the Latin *incomitatus,* unaccompanied, alone; only a single specimen is known.

BIOLOGY: The single pupa of this species was found in a large mountain stream with rocky bottom, where many other species of *Gigantodax* and *Simulium* occurred. The pupa adhered to the undersurface of a large stone; the water temperature was 15°C. All other black fly species found here were collected in considerable numbers. As we found only a single specimen of *incomitatus,* we assume that this location is marginal to the geographical or ecological range of the species, or that it was a seasonal period of low abundance.

DISCUSSION: *G. incomitatus,* to judge from the pupa, seems to be close to *G. bettyae* and *G. septenarius*; it differs from both of them by the much more slender gill branches and the absence thereon of cuticular processes. Unfortunately, the absence for study of females and larvae adds to the uncertain taxonomic position of this species.

Gigantodax pennipunctus Enderlein

Figures 94A–M, 95A–K, 96A–I, 97A–D, 98A–Q

Gigantodax pennipunctum Enderlein, 1934: 274. Smart, 1945: 499. Vulcano, 1967: 3; 1977, 290. [Incorrect gender]

DIAGNOSIS: *G. pennipunctus* differs from all other *Gigantodax* by the structure of the pupal gill which is basally stout with very short tegumentary processes and apically with deciduous filaments.

REDESCRIPTION: *Female.* Length of wing 4.1–4.3 mm. Head dark brown, clypeus light brown. Antennae entirely light orange, scapus and pedicellus not lighter than remaining segments; most of first flagellomere distinctly darker than remaining segments. Maxillary palp and proboscis brown. Hairs of head brass colored. Scutum light yellowish brown, with median longitudinal stripe conspicuously darker; width of median stripe about one-fourth of total width of scutum. Scutellum whitish yellow; metanotum as dark as me-

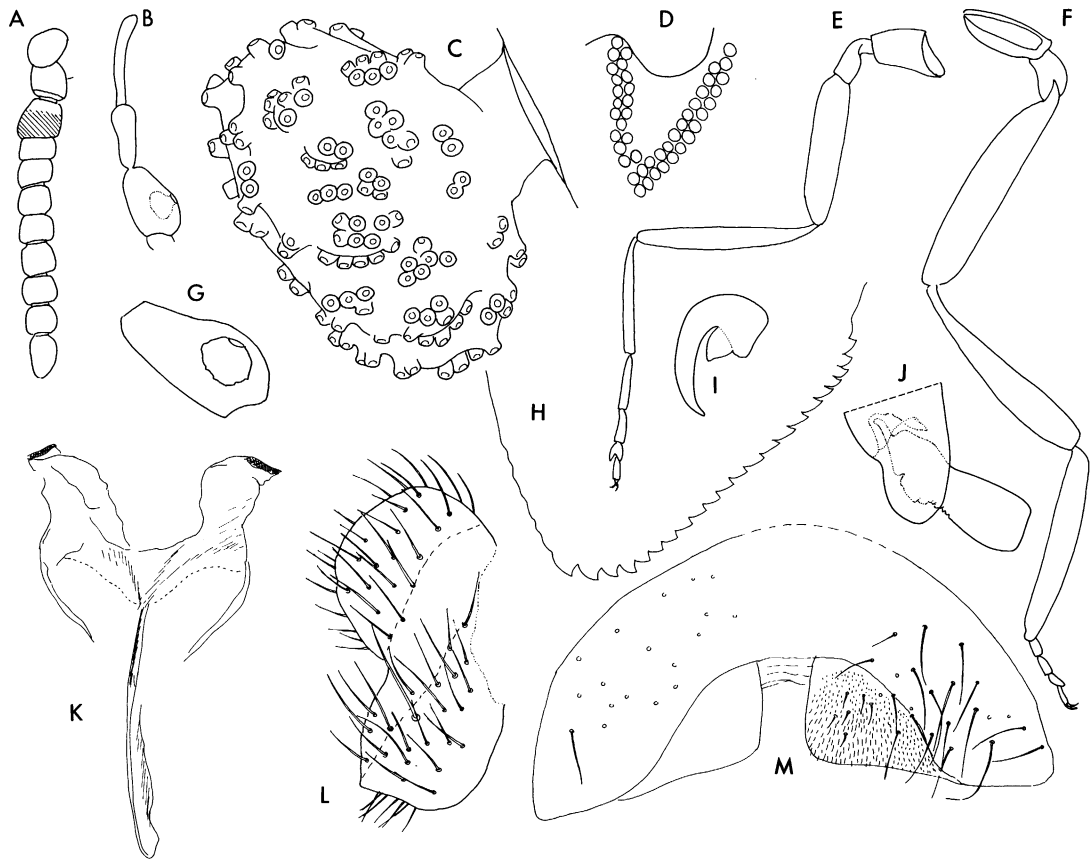

Fig. 94. *Gigantodax pennipunctus.* Female. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle of maxillary palp. **D.** Fronto-ocular triangle. **E.** Foreleg. **F.** Hind leg. **G.** Second article of maxillary palp. **H.** Apical portion of mandible. **I.** Claw. **J.** Calcipala, with second tarsal article. **K.** Genital fork. **L.** Cercus and paraproct. **M.** Sternite VIII and gonapophyses.

dian stripe of scutum. Pleural region light yellowish brown, somewhat darker on upper portion. Thoracic setae on stem vein dark, with reddish tinge; setae on other veins brown. Halteres faintly pigmented, capitulum white. Legs very pale yellow; last tarsal segment conspicuously darkened; setae of legs concolorous. Abdominal tergites irregularly spotted with piceous anteriorly and at sides, but most of disc ivory colored; apical segment entirely dark. Abdominal hairs of abdomen silver colored.

Frontal angle 65°. Fronto-ocular triangle slightly higher than wide at base (fig. 94D). Shape and proportions of antennal segments as shown in figure 94A. Mandible with teeth only on inner margin, outer margin slightly crenulated (fig. 94H); number of teeth 23–24. Maxilla with 23–24 teeth. Last segment of maxillary palp (fig. 94B) almost twice as long as penultimate. Second segment of maxillary palp broadly oval; narrowed on apical portion (fig. 94G); ratio length/width = 1:0.54–0.57. Sensory vesicle from subglobular to ovoid, with very short neck (fig. 94C). Sc with 27–31 hairs. R with setae arranged in two to three irregular rows. R_1 with setae in one or two rows; spinules present, well developed, beginning at level of insertion of Sc on C in one row, not more numerous than setae. Setae of R_s in one row on apical portion of upper surface of vein, in several rows on entire undersurface. A_1 not reaching wing margin. Shape and proportions of fore and hind leg

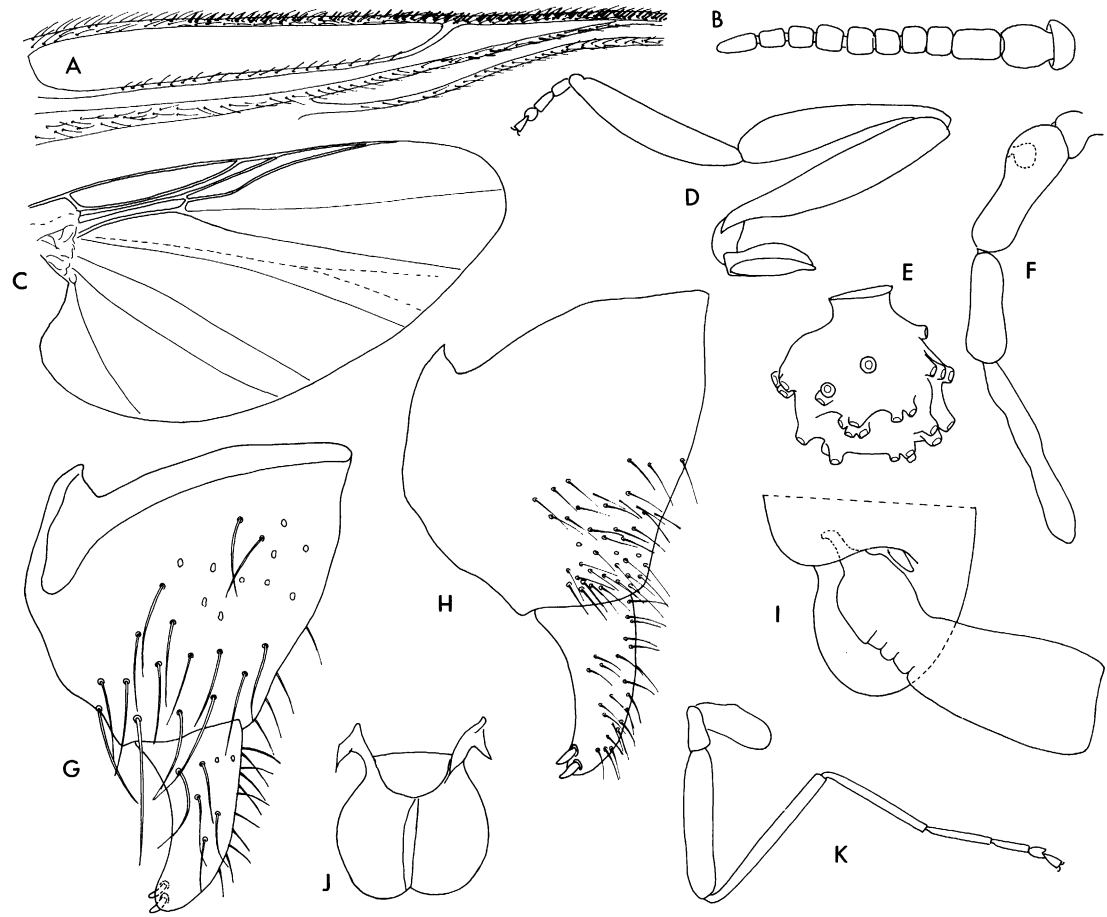

Fig. 95. *G. pennipunctus.* Male. **A.** Anterior area of wing. **B.** Antenna. **C.** Wing. **D.** Hind leg. **E.** Sensory vesicle of maxillary palp. **F.** Maxillary palp. **G.** Basimere and distimere, under surface. **H.** Same, upper surface. **I.** Calcipala and second tarsal segment. **J.** Ventral plate. **K.** Foreleg.

segments as in figure 94E, F. Hind basitarsus 6.4–7.0 times as long as wide. Calcipala reaching center of second tarsomere (fig. 94J). Basal tooth of claw short (fig. 94I). Abdominal sterna only with simple hairs. Eighth sternite, gonapophyses, genital fork, and cercus with paraproct as illustrated (fig. 94K–M).

Male. Length of wing 3.8–4.0 mm. General color as in female, except as follows: pedicellus and base of first flagellomere distinctly lighter than flagellum, the latter in many specimens with grayish tinge, and most of first flagellomere conspicuously darker than rest of flagellum, as in female; scutum from yellowish brown to rust colored, white median longitudinal stripe distinct; abdominal terga piceous, only narrow hind margin whitish, in some specimens light color invading small portions of center of disc of tergites.

Holoptic. Shape and proportions of antennal segments as in figure 95B; ratio length/width of first flagellomere 1:0.67–0.71. Apical segment of maxillary palp almost twice as long as penultimate (fig. 95F). Sensory vesicle small, subglobular, with distinct neck (fig. 95E). Wing much as in female; Sc with 17–20 setae (fig. 95A). Shape and proportions of leg segments as in figure 95D, K. Fore basitarsus 12.0–12.5 times, hind basitarsus 5.16–5.30 times as long as wide. Calcipala (fig. 95I) reaching level of center of second tarsomere.

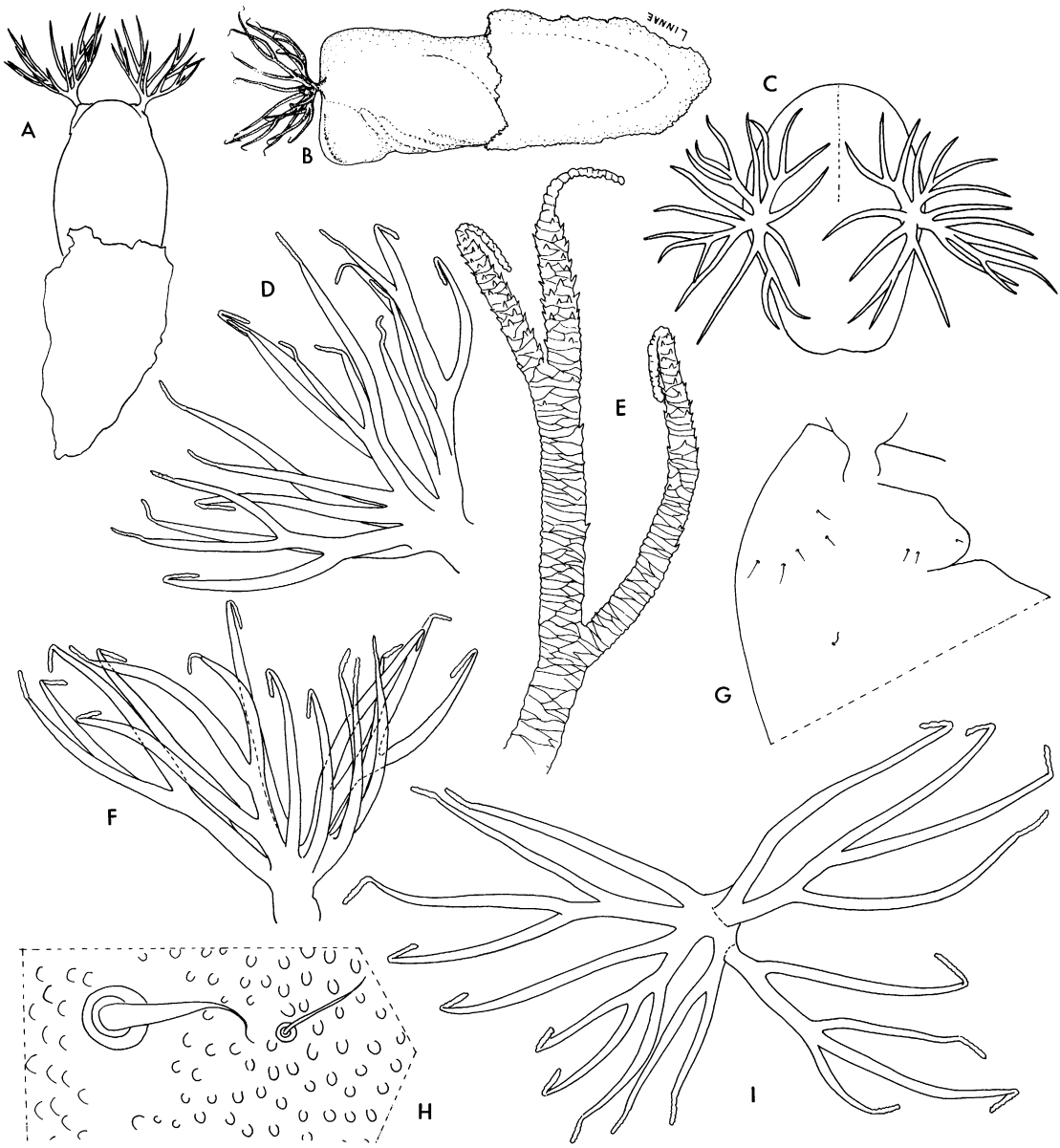

Fig. 96. *G. pennipunctus.* Pupa. **A.** Pupa in cocoon, dorsal view. **B.** Same, laterally. **C.** Frontal view with gills. **D.** Gill, with terminal filaments. **E.** Distal portion of gill branches, with terminal filaments. **F.** Gill. **G.** Part of thorax, with trichomes. **H.** Abdominal tergite III, with setae and platelets. **I.** Gill.

Distimere slightly over half as long as basimere, with two apical spines (fig. 95G, H). Main body of ventral plate slightly wider than long, its sides rounded. Ventral plate as in figure 95J.

Pupa. Cocoon small, only covering part of abdomen, with first and second abdominal tergites, thorax, head, and gills exposed (fig. 96A, B). Cocoon consisting of irregular mesh, in all specimens examined incrusted with fine detritus. Length of cocoon about 3.0 mm. Total length of body of pupa about 4.0 mm; cephalopterothecal length 2.6–2.7 mm. Gills small, shorter than cephalopterothecal length,

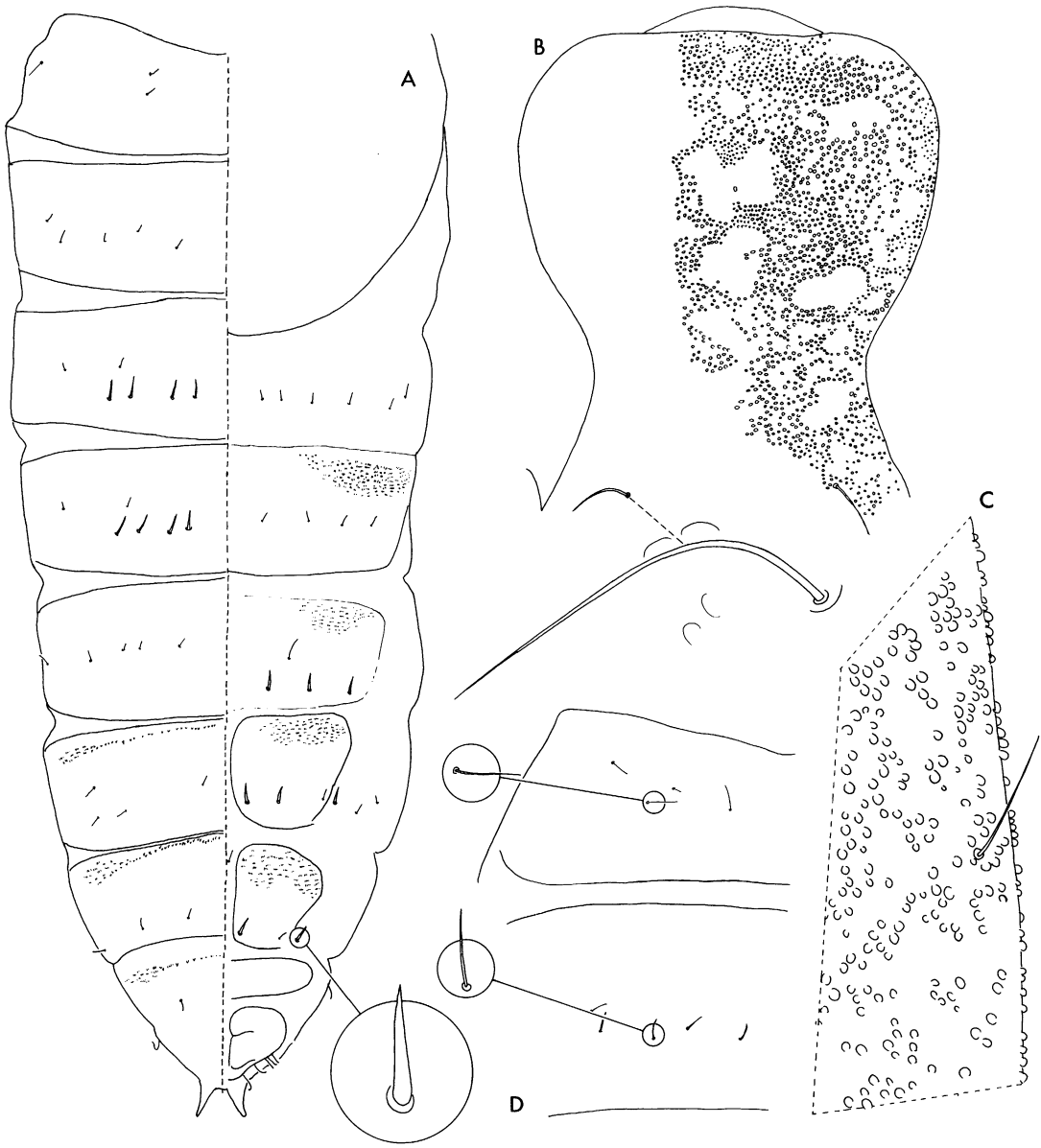

Fig. 97. *G. pennipunctus.* Pupa. **A.** Abdomen, tergites at left, sternites at right. **B.** Frontoclypeus of female. **C.** Surface structure of thorax, with platelets and trichome. **D.** Chaetotaxy of abdominal tergites I and II.

each with 18 short, rigid branches; each gill in shape of forwardly directed basket (figs. 96A–F, I, 98P). Branches stout at base, conspicuously tapering toward apex, distally with short, caducous respiratory filament. Surface of branches minutely dotted, dots aggregated to form transverse wrinkles and with small cuticular processes (fig. 96E). Apical portion of branches as follows: one dorsal and one ventral branch, both simple; two dorsal, one lateral, and one ventral primary branch, all variously divided. Upper dorsal and ventral primary branches each with three secondary branches; outer dorsal primary branch with

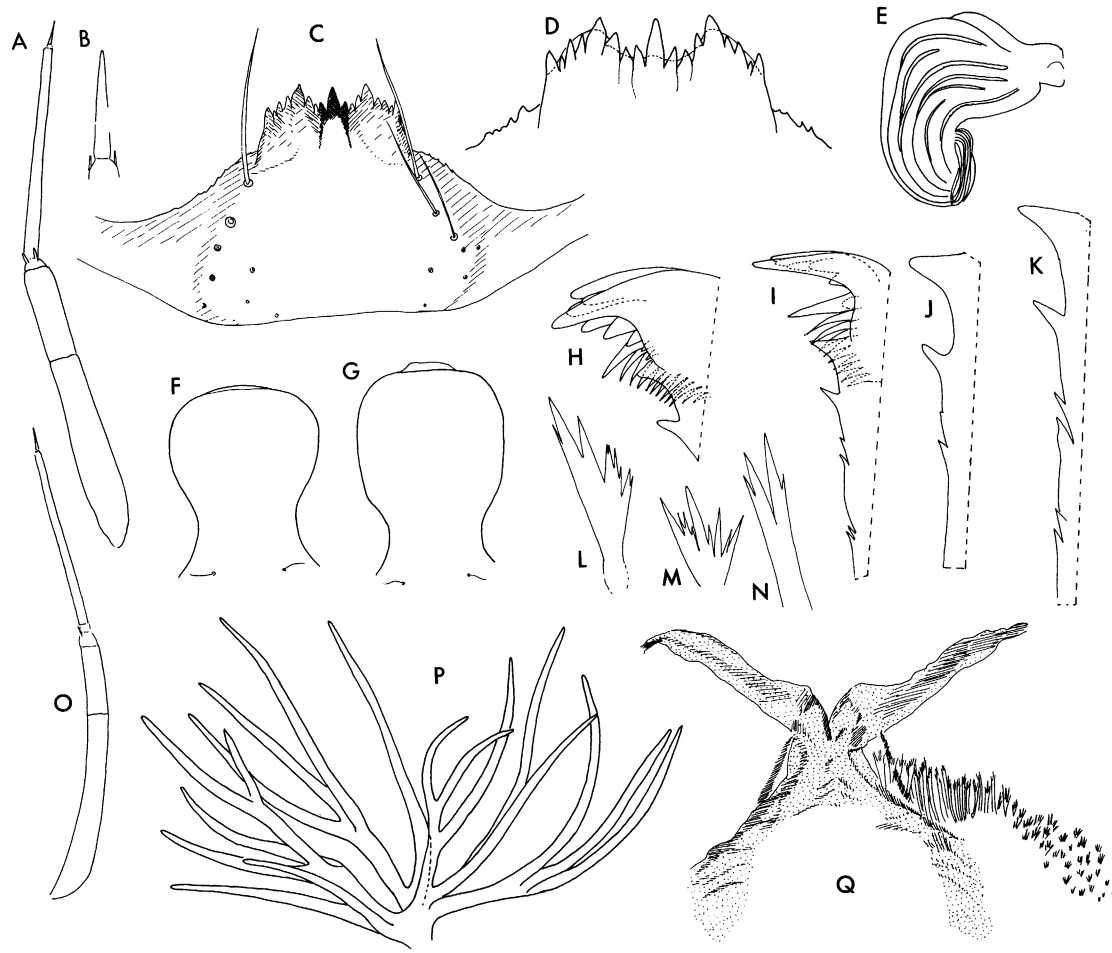

Fig. 98. *G. pennipunctus.* A–E. Larva. **A.** Antenna. **B.** Terminal sensillum of antenna. **C.** Hypostomium. **D.** Anterior portion of hypostomium. **E.** Gill histoblast. **F.** Outline of frontoclypeus of female. **G.** Same, male. H–O. Larva. **H, I.** Apex of mandible. **J, K.** Mandibular serrations. **L–N.** Scales of anal sclerite. **O.** Antenna. **P.** Pupal gill. **Q.** Detail of anal sclerite.

four secondary branches, and lateral primary branch with six secondary branches. Frontoclypeus of female and male as in figure 98F, G, with very numerous, somewhat faint, glabrous platelets. Facial trichomes in shape of long slender hairs (fig. 97B). Thorax trichomes as in figure 96G. Thorax with platelets glabrous, arranged as in figure 97C. Dorsocentral and dorsolateral trichomes hairlike, short. Setae of abdominal tergite I hairlike, length 28–30 μm; setae of tergite II similar, only slightly longer, 28–35 μm (fig. 97D). Tergites III and IV each with 4 + 4 hooks with narrowly drawn out point (figs. 96H, 97A). Anterodorsal seta inconspicuous, very fine, hairlike. Setae of tergites V–VIII inconspicuous, length on tergite VII 35–40 μm. Spinecombs on tergites VI–VIII, on VI and VII poorly developed, difficult to perceive, those on tergite VII consisting of 23–25 very irregularly arranged spines, length not more than 5 μm, viz., about one-seventh of setal length on this tergite. Specialized setae of eighth and ninth segments straight or slightly curved, not branched. Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VII glabrous.

Mature larva. Length 8.0–8.2 mm; width of head capsule 0.8 mm. Body shape as usual

for the genus; ventral papillae well developed. Color of larva whitish, with faint overall brownish tinge. Head light yellow, with pattern of cephalic apotome conspicuous; area of hypostomial bridge almost imperceptibly darkened, with faint median longitudinal stripe whitish. Antenna approximately as long as stem of cephalic fan, faintly pigmented third segment not distinctly darker than preceding. Shape of antenna as in figure 98A, O; ratio of segments I–III = 1:0.37–0.58:0.94–1.30. Terminal sensillum of antenna almost six times as long as wide at base (fig. 98B). Cephalic fans with 26–29 large rays, their teeth as usual in *Gigantodax*. Mandible (figs. 98H–K) with 9–10 inner teeth and 5–6 marginal serrations. Maxillary palp 2.8 times as long as wide at base. Hypostomium as illustrated (fig. 98C, D). Median tooth reaching level of corner tooth apex. Line connecting apices of fourth lateral tooth and corner tooth meeting at angle of about 110°; 6–7 lateral serrations and 4–6 hypostomial setae in each row. Cervical sclerite as in *G. cormonsi*. Gill histoblast as in figure 98E, dark brown in fully mature specimens. Perianal scales extremely well developed, those between arms of X-shaped sclerite unusually elongate (fig. 98L–N, Q). Scales forming complete circumanal ring. Recurrent struts narrow, distinct. Crochet ring with 100–107 rows of 18–20 hooks.

MATERIAL EXAMINED: PERU: *Cuzco:* city of Cuzco on hillside 500 m from termination of Sapsi Street, 3300 m, Aug. 12, 1965 (P. and B. Wygodzinsky; AMNH), 21 males, 13 females (reared, and with their associated pupal exuviae), pupae, and larvae; Huampar, 3450 m, April 19, 1971 (S. Coscarón; MLP), 1 male (reared, and with associated pupal exuviae), pupae, and larvae.

BIOLOGY: The specimens found in the city of Cuzco were located in a water trickle of high mineral content, not more than 1 in. deep; its temperature was about 15°C. The water formed thick mineral deposits on all objects in its course, including live pupae of *G. pennipunctus,* in many cases covering not only the cocoon but also the exposed portion of the pupae, including the gills. Larvae and pupae were found on the undersurfaces of small stones and dead eucalyptus leaves. Pupae collected at Huampar were equally covered by mineral deposits.

DISCUSSION: *G. pennipunctus* was described from Cuzco; we have not examined the original material. Our specimens are determined as *pennipunctus* because they are topotypical and fit the original description in size and all chromatic characters. Enderlein's description states that the calcipala extends beyond the center of the second tarsomere; in slide-mounted specimens, the calcipala reaches but does not surpass the center of the second tarsomere.

The character chosen by Enderlein to select the specific name of this species, viz., the dark spot apparent on r-m is not unique for the species, and is found to a greater or lesser degree also in other species of the genus. The main feature distinguishing *pennipunctus* from all other members of the genus is the pupal gill structure.

As it is not easy to put *pennipunctus* in a species group, we include it here with reserve. The greatest differences with the typical species of the *cilicinus* group are in the larva, e.g., the median tooth does not surpass the level of the corner teeth, a second antennal article is relatively shorter than the first, recurrent struts are not well pigmented distally, mandible has fewer marginal serrations, crochet ring has fewer rows and hooks; also there are minor differences in the adults, e.g., showing longer calcipala. Gill branches of the pupa differ especially in the length of the cuticular projections. *Gigantodax pennipunctus* is the only known species with thick and tubular branches possessing rough cuticular projections, which could be the initial transformation of the hairlike projections state found in the *cilicinus* group.

Gigantodax arrarteorum, new species

Figures 99A–U, 100, 101A–H, 102A–I, 103A–M

DIAGNOSIS: Distinguished from *G. cilicinus* by the number of hooks on the abdominal sternites of the pupa, as described and illustrated, as well as by the seventh and eighth gill branches of the pupa arising from a common trunk, as opposed to *cilicinus* where the sixth and seventh branches share a common trunk; *arrarteorum* differs from the closely related *clandestinus* as shown under the heading of the latter species.

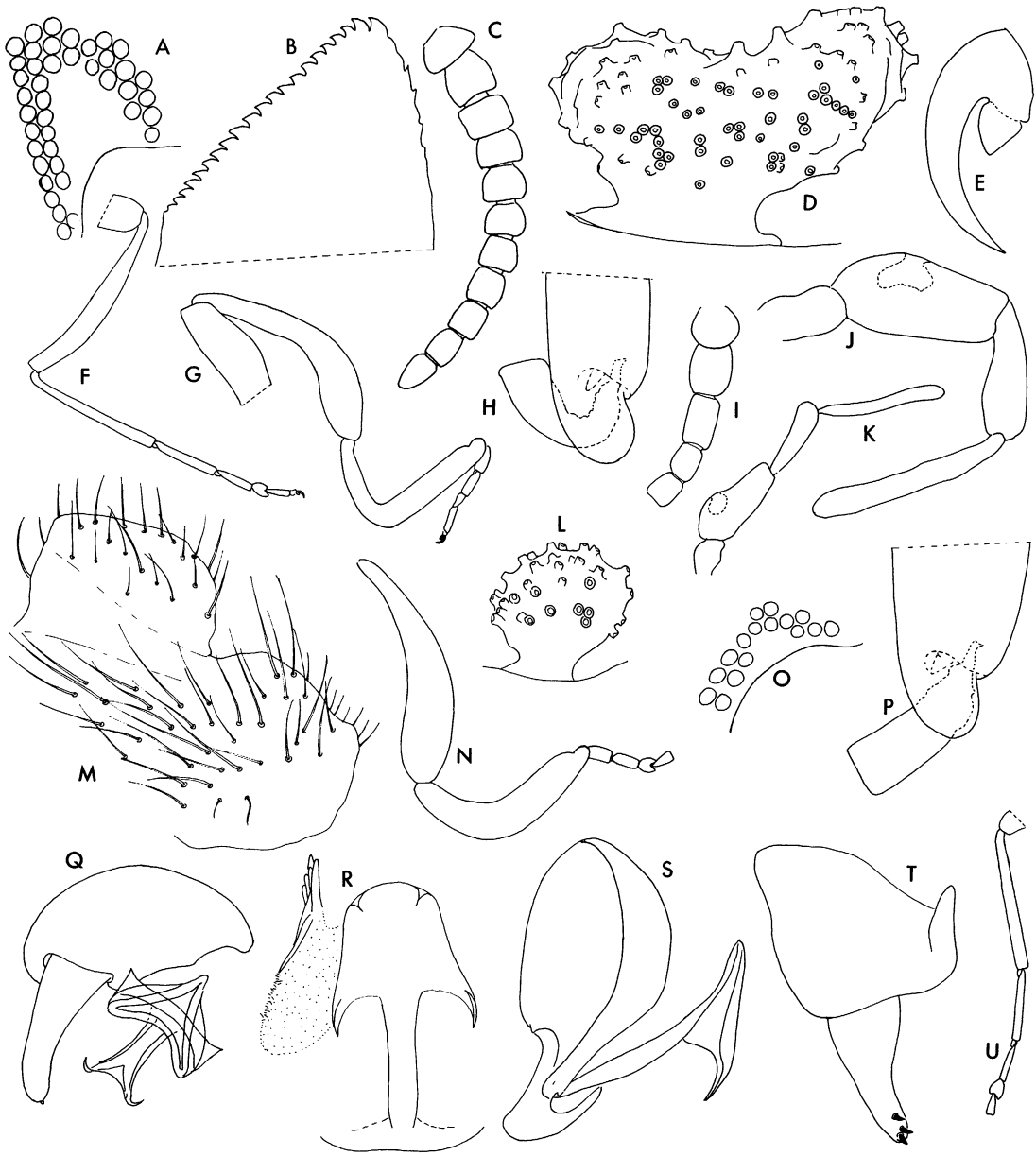

Fig. 99. *Gigantodax arrarteorum.* A–J. Female. **A.** Fronto-ocular triangle. **B.** Apex of mandible. **C.** Antenna. **D.** Sensory vesicle of maxillary palp. **E.** Claw. **F, G.** Some articles of fore and hind legs. **H.** Calcipala. **I.** Basal portion of antenna, male. **J.** Maxillary palp. K, L. Male. **K.** Maxillary palp. **L.** Sensory vesicle of maxillary palp. **M.** Female, cercus and paraproct. N–U. Male. **N.** Hind leg. **O.** Fronto-ocular triangle. **P.** Calcipala, with second tarsal segment. **Q.** Basimere, distimere, ventral plate, and median sclerite. **R, S.** Median sclerite, different views. **T.** Basimere and distimere. **U.** Portion of foreleg.

DESCRIPTION: *Female.* Length of wing 5.2 mm. Head black; pilosity brass colored. Antenna orange, with short silvery pubescence, more dense toward apex of antennae; scapus and pedicellus not conspicuously lighter than adjoining segments. Maxillary palp piceous. Scutum dark purple, reddish orange anteriorly at center; pronotal sclerites yellowish.

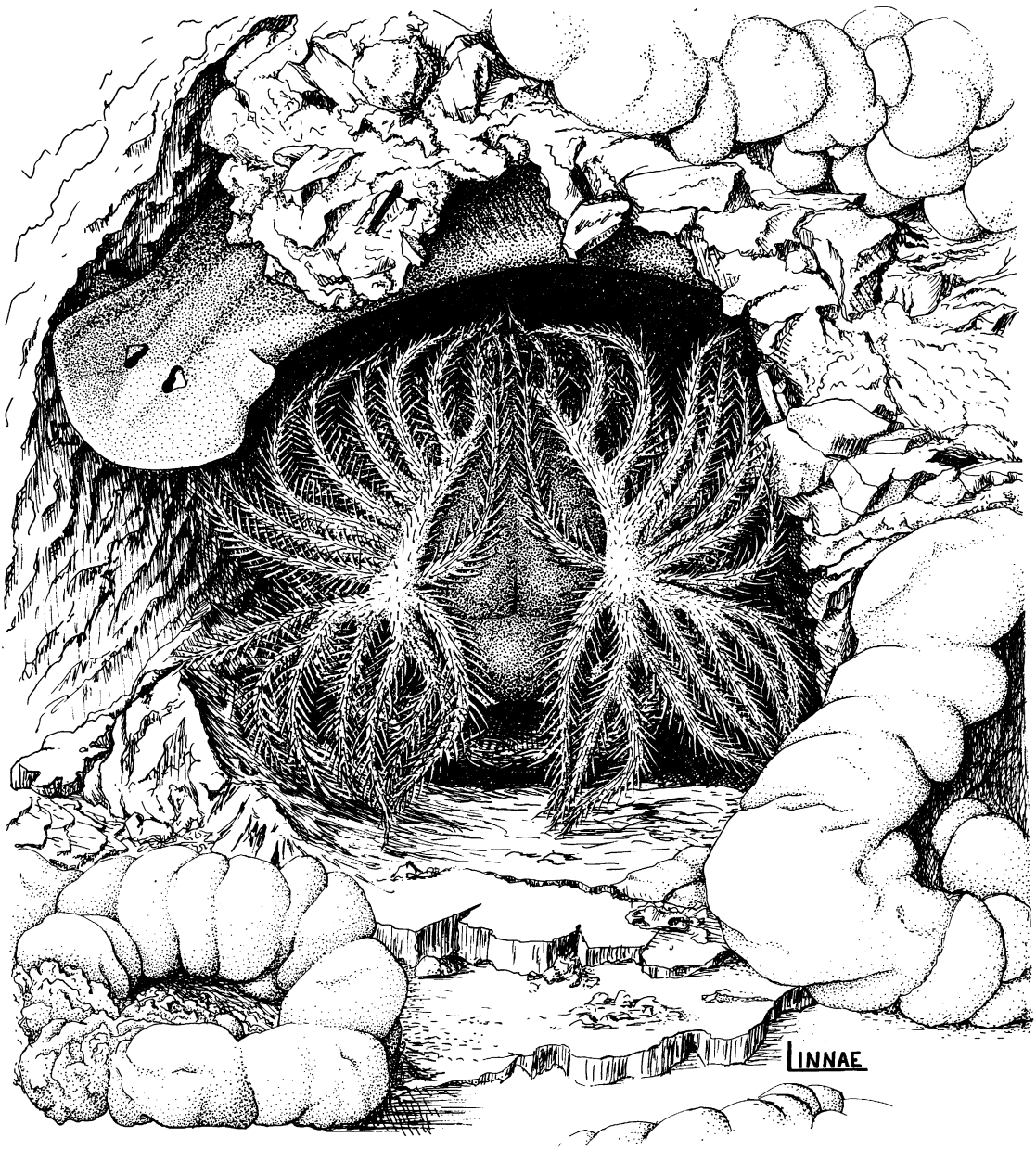

Fig. 100. *G. arrarteorum.* Pupa. Frontal view in natural habitat.

Scutellum and metanotum as in scutum. Pleuron purple on upper portion, changing to light brown on lower portion. Thoracic setae golden colored, those of scutum iridescent. Wing translucent; all veins light brown. Setae on stem-vein light or dark brown, changing with illumination type. Halter whitish, extreme base and capitulum tinged with brown. Legs yellowish brown, setae concolorous. Abdominal tergites I–V piceous; tergites VI–VIII light grayish brown, their posterior margin narrowly whitish. Hairs of abdomen from brass to golden colored.

Frontal angle approximately 55°. Frontoocular triangle slightly higher than wide (fig. 99A). Shape and proportions of flagellomeres

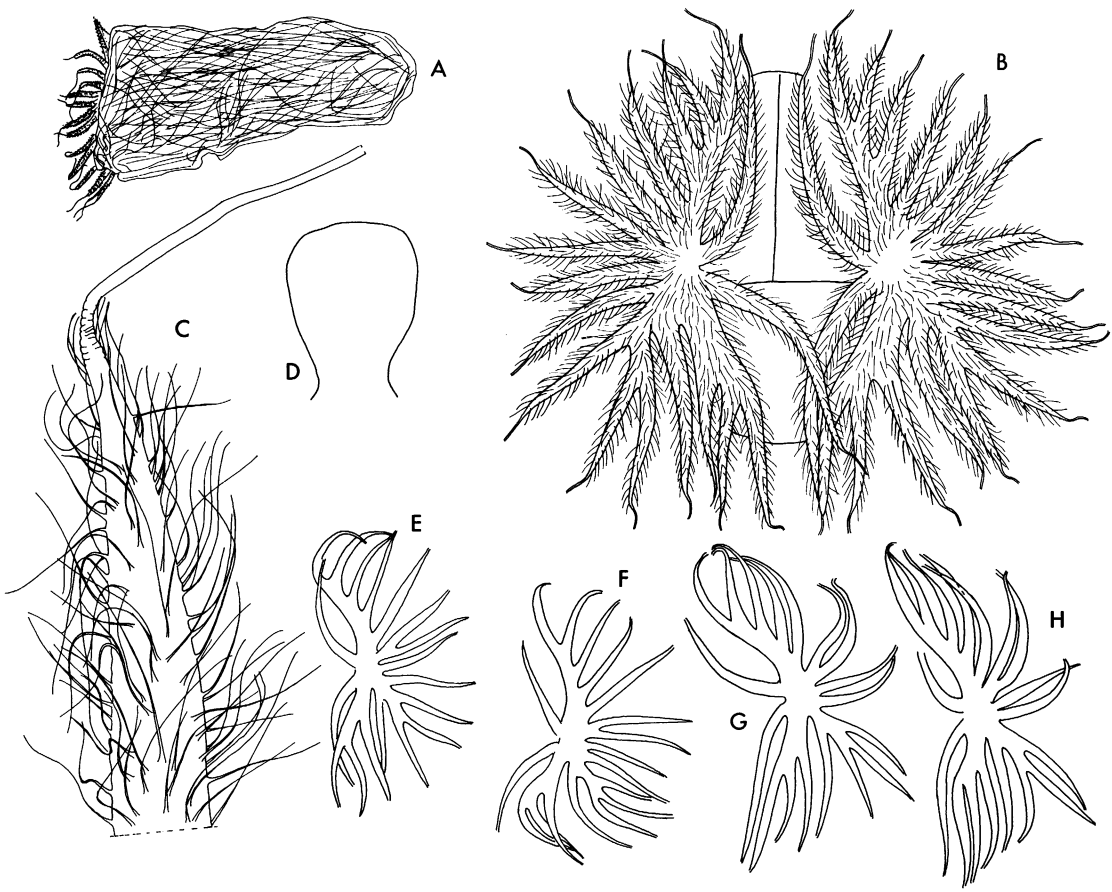

Fig. 101. *G. arrarteorum.* A–H. Pupa. **A.** Pupa in cocoon, lateral view. **B.** Gills, frontal view. **C.** Detail of distal branch of gill with the cuticular processes. **D.** Outline of male frontoclypeus. **E–H.** Aspect of gills.

as in figure 99C. Mandible with approximately 21 teeth on inner margin; outer margin (in single specimen examined) irrregularly but distinctly crenulated near apex (fig. 99B). Maxilla with 26–28 teeth. Last segment of maxillary palp 1½ times as long as penultimate (fig. 99J). Second segment of maxillary palp elongate oval, ratio length/width 1:0.56. Sensory vesicle large, with short but distinct neck (fig. 99D). Sc with 34 or 35 hairs. R with setae in two or three irregular rows. R_1 with setae in two irrregular rows; spinules well developed, beginning at level of insertion of Sc on C, becoming more numerous toward apical half of vein, numbering from 12 to 20. R_s with setae on undersurface basally in one or two, apically in three irregular rows; on upper surface setae in one row except on bare basal half. A_1 almost reaching wing margin. Shape and proportions of fore and hind leg segments as in figure 99F, G. Hind basitarsus 7.4 times as long as wide. Calcipala covering almost half the length of second tarsomere (fig. 99H). Basal tooth of claw, small (fig. 99E). Paraproct and cercus as in figure 99M.

Male (pharate). Length of wing somewhat more than 5.0 mm. Color unknown. Very small fronto-ocular area present (fig. 99O). Shape and proportions of some antennal segments in figure 99I; ratio length/width of first flagellomere 1:0.63–0.71. Last segment of maxillary palp 1½ times as long as penultimate (fig. 99K). Sensory vesicle subglobular,

Fig. 102. *G. arrarteorum.* Details of pupa. **A.** Dorsocentral trichome of thorax, with area of insertion. **B.** Frontoclypeus of female with platelets. **C.** Facial trichome of base of frontoclypeus. **D.** Portion of thorax, with trichomes. **E.** Chaetotaxy of first and second abdominal tergites. **F.** Anterolateral trichome of abdominal sternite III. **G.** Terminal spine of apex of abdomen. **H.** Hook of tergite IV. **I.** Dorsolateral trichome of thorax, with platelets.

with distinct neck (fig. 99L). Wing as in female, but Sc only with 25 hairs. Shape and proportions of fore and hind leg segments as in figure 99N, U. Fore basitarsus 12.0, hind basitarsus approximately 5.8 times as long as wide. Calcipala almost reaching middle of second tarsomere (fig. 99P). Genitalia as in figure 99Q–T. Distimere about as long as basimere, with three apical spines (fig. 99T).

Pupa. Cocoon covering entire body of pupa

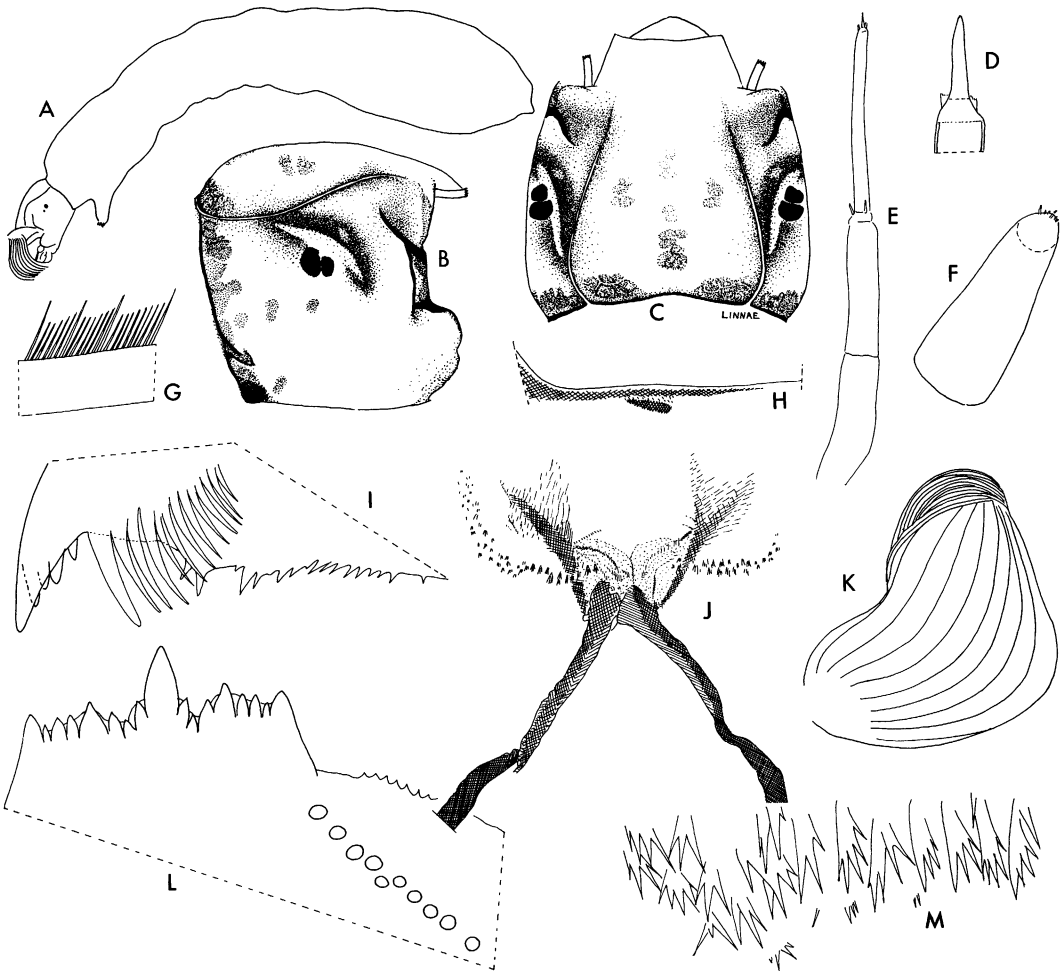

Fig. 103. *G. arrarteorum.* Larva. **A.** Larva, lateral view. **B.** Head, lateral view. **C.** Head, dorsal view. **D.** Apical sensillum of antenna. **E.** Antenna. **F.** Maxillary palp. **G.** Teeth of rays of cephalic fan. **H.** Cervical sclerite. **I.** Apex of mandible. **J.** Portion of anal sclerite. **K.** Gill histoblast. **L.** Detail of hypostomium. **M.** Scalelike setae of anal area.

except head and gills, but in many specimens only covering abdomen and part of thorax (fig. 101A). Color of cocoon whitish, appearing parchmentlike, tightly woven but clearly with individual threads. Fabric of cocoon tightest on basal, more loose on apical portion, faintly translucent along entire extension. Length of complete cocoon up to 5.5 mm. Length of pupal body up to 5.4 mm; cephalopterothecal length 3.1–3.2 mm. Gill light brown, compact, consisting of 18 branches originating from a common base, branches thick basally, gradually tapering toward pointed ends and with apical respiratory filaments. Branches completely covered with long hairlike cuticular processes (figs. 100, 101B, C, E–H). All branches situated on one plane, perpendicular to longitudinal axis of body and pupa together; both gills starlike in appearance (figs. 100, 101B). Secondary branches of more uniform size than in *cilicinus.* Branches 2–6 arising consecutively from common trunk, seventh and eighth from extremely short common trunk. Shape of frontoclypeus as in figures 101D, 102B. Shape and proportions of platelets of frontoclypeus irregularly distributed, single, or forming clusters. Facial trichomes hairlike (fig. 102C).

Disposition of thoracic trichomes as in figure 102D. Dorsocentral trichomes (fig. 102A) in shape of slender setae; dorsolateral trichomes (fig. 102I) hairlike. Setae of first abdominal tergite hairlike, length 50–62 μm; setae of tergite II stouter and longer (65–81 μm) (fig. 102E). Tergites III and IV each with 4 + 4 short hooks; anterodorsal setae strong, longer than hooks (fig. 102F). Hook of tergite IV as in figure 102H. Length of setae of tergite VI 61–80 μm. Spine-combs on tergites VI–VIII entire or interrupted, consisting on tergite VII of 28–33 spines, length 21–32 μm, viz. from one-half to one-third of length of setae of this tergite. Specialized setae of abdominal apex absent. Sternite IV with a few short strong setae. Sternite V with 3 + 3, VII with 2 + 2 short hooks; pleural membranes of segments V–VII with one or two hooks and one or two stout spinelike setae. Sternite VIII glabrous. Terminal hook of abdomen as in figure 102G.

Mature larva. Length 10 mm; width of head capsule 1.0 mm. Body shape (fig. 103A) as usual for the genus; ventral papillae present. Color brownish, with hypodermal pigment most intense on dorsum of posterior half of body. Head light brown; spots of cephalic apotome conspicuous; posterolateral spots completely separated, transverse diameter of spots larger than space separating spots (fig. 103C). Distribution of pigment on sides of head as in figure 103B, more extensive than in *cilicinus.* Hypostomial bridge darkened, with faint median longitudinal band whitish. Antenna as long as stem of cephalic fan, distinctly although lightly pigmented, third segment not darker than remaining. Shape of antenna as in figure 103E; ratio of segments I–III = 1:0.8–0.9:1.1–1.2. Terminal sensillum (fig. 103D) four times as long as wide at base. Cephalic fans with 25–29 large rays, their teeth as in figure 103E. Mandible (fig. 103I) with 11–14 inner teeth and 16–19 marginal serrations. Maxillary palp 2½ times as long as wide at base (fig. 103F). Hypostomium as in figure 103L; general structure as in *cilicinus,* with 12–27 lateral serrations and 9–11 hypostomial setae arranged in one or two irregular rows. Cervical sclerites with oval platelets close to but not fused with narrow transverse sclerotized bands (fig. 103H). Histoblast as in figure 103K. Anal sclerite and perianal scales as in figure 103J, M. Crochet ring with approximately 150 rows of 22–25 hooks each. Recurrent struts well developed. Rectal gills not seen.

HOLOTYPE: PERU: *Junin:* Tarma: Chacabamba, on road from Palcomayo to San Pedro de Cajas and Junin, 3700 m, July 15, 1965 (P. and B. Wygodzinsky; AMNH), one pharate male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, one female (reared, and with associated pupal exuviae), paratype; AMNH, pupae, and larvae; one pharate female.

ETYMOLOGY: The species is named for Dr. Juana and Dr. Juan Arrarte, of Lima, Peru, who did so much to make the first author's sojourn in Peru most profitable.

BIOLOGY: The larvae and pupae of this species were found exclusively on the underside of large boulders resting on the bottom of a clear stream approximately 1 m wide and 25 cm deep, in a high mountain pasture; the water temperature was 10°C. The larvae shared this habitat with those of *G. chacabamba.* Pupae of *G. arrarteorum* were in most cases wedged in cracks or fissures of the large stones where they were found, with only the striking light-colored gills visible (fig. 100).

DISCUSSION: The most striking feature of *arrarteorum,* as compared to *cilicinus,* is the multiplication of hooks on abdominal sternal plates VI and VII; this apomorphic character is shared with *G. clandestinus* as described below.

Gigantodax clandestinus, new species

Figures 104A–S, 105A–N, 178E

DIAGNOSIS: One of the largest species, color dark purple, pupal gill with 18 stout branches abruptly tapering apically and covered by thin filaments, larva with median tooth distinctly projecting beyond level of corner teeth.

DESCRIPTION: *Female.* Length of wing 6.0 mm. Color as in *arrarteorum.* Shape of front as in figure 104E. Frontal angle approximately 55°. Fronto-ocular triangle about as high as wide (fig. 104B). Shape and proportions of antennal segment as in figure 104A. Mandible with 27–32 teeth on inner margin; outer margin smooth. Maxilla with 29–34 teeth. Distal segment of maxillary palp about 1.5 times as long as penultimate. Second seg-

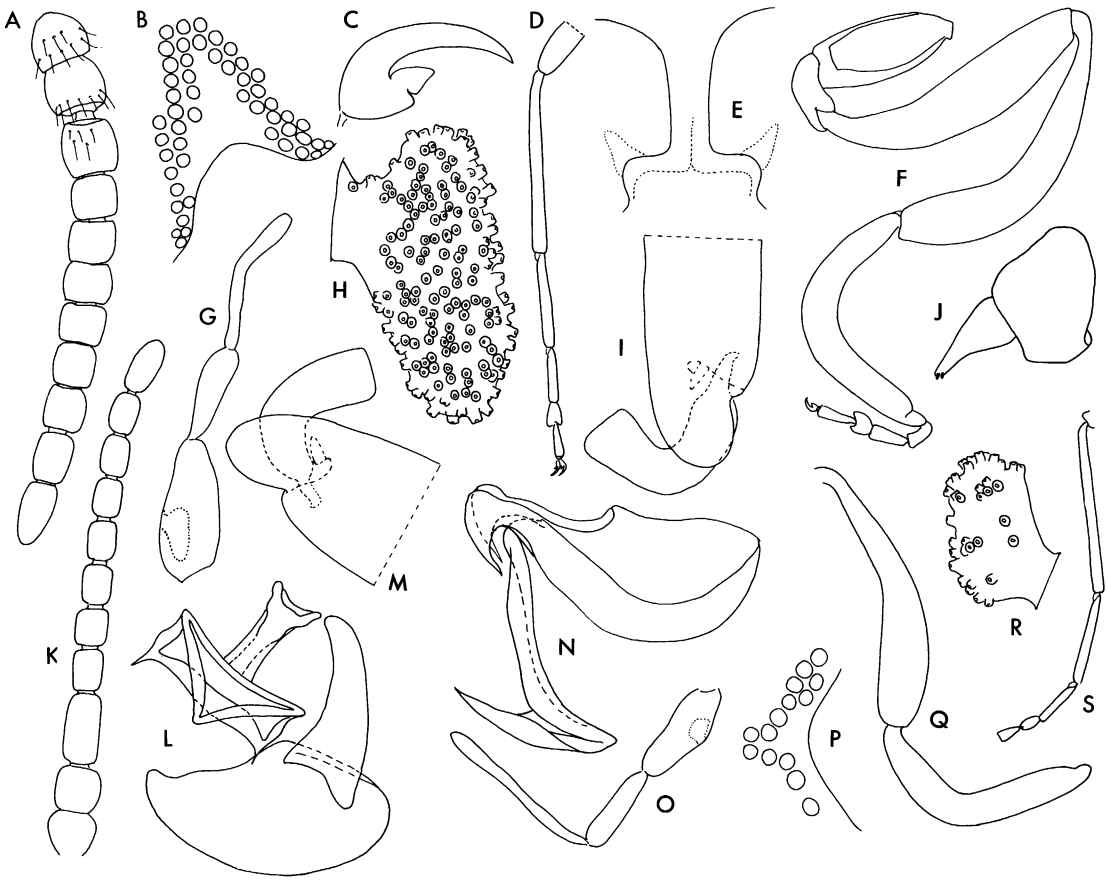

Fig. 104. *Gigantodax clandestinus.* A–H. Female. **A.** Antenna. **B.** Fronto-ocular angle. **C.** Claw. **D.** Foreleg. **E.** Frons. **F.** Hind leg. **G.** Maxillary palp. **H.** Sensory vesicle of maxillary palp. **I.** Calcipala. J–S. Male. **J.** Basimere and distimere. **K.** Antenna. **L.** Median sclerite and ventral plate, sublateral aspect. **M.** Calcipala. **N.** Median sclerite and ventral plate, side view. **O.** Maxillary palp. **P.** Fronto-ocular triangle. **Q.** Femur and basitarsus of hind leg. **R.** Sensory vesicle of maxillary palp. **S.** Tarsus of foreleg.

ment of palp elongate, conspicuously tapering apically (fig. 104G). Sensory vesicle (fig. 104H) elongate oval. Wing setae as in *arrarteorum.* Shape and proportion of fore and hind leg segments as in figure 104D, F. Calcipala covering less than half the length of second tarsomere (fig. 104I). Basal tooth of claw as illustrated in figures 104C, 178E. Genitalia as in *arrarteorum.*

Male. Length of wing 6.2 mm. Color as in female, but scutum, scutellum, and metanotum dark reddish brown. Very small fronto-ocular area present (fig. 104P). Shape and proportions of antennal segments as in figure 104K; ratio length/width of first flagellomere 1:2.1–2.2. Distal segment of maxillary palp (fig. 104O) almost twice as long as penultimate. Sensory vesicle (fig. 104R) oval, with distinct neck. Wings as in *arrarteorum.* Shape and proportions of some leg segments as shown in figure 104Q–S. Ratio length to width of fore basitarsus 14.0, of hind basitarsus approximately 6.5. Calcipala covering approximately half the length of second tarsomere (fig. 104M). Genitalia (fig. 104J, L, N) similar to those of *arrarteorum,* but distimere only with two apical spines, and ventral plate appearing wider.

Pupa. Cocoon as in *arrarteorum,* its maximum length 6 mm. Length of body up to 6.2

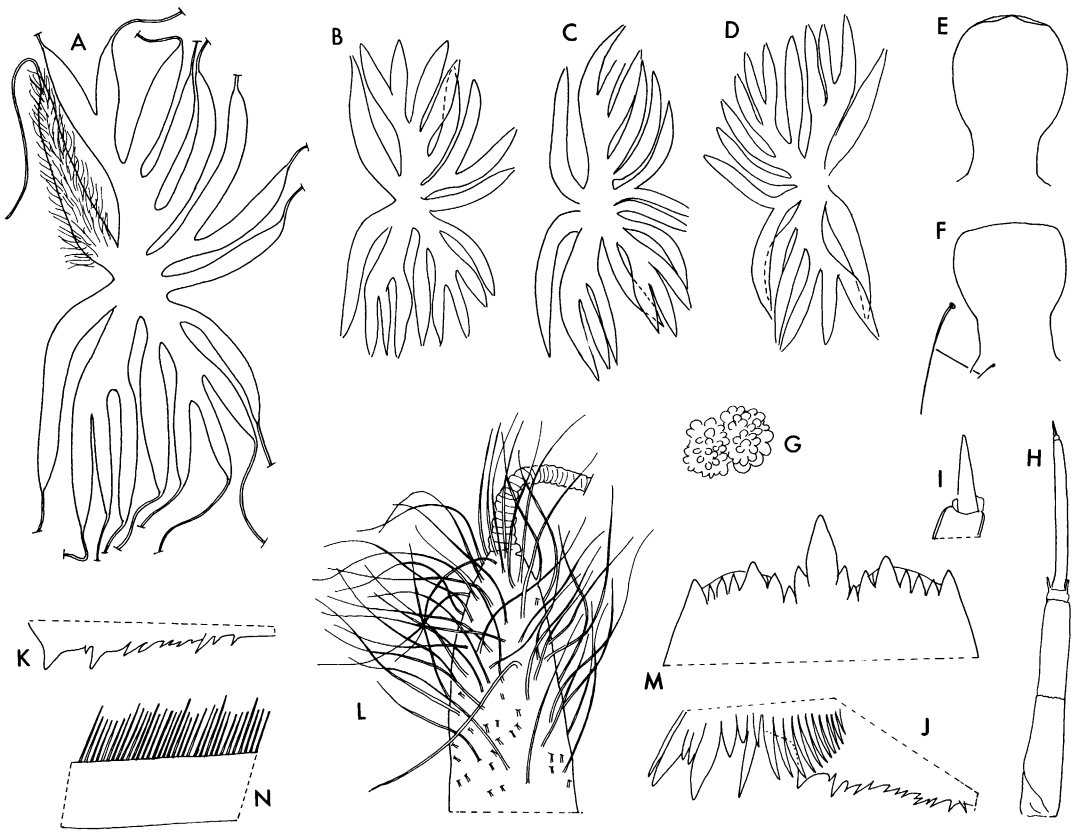

Fig. 105. *G. clandestinus.* Pupa. **A–D.** Gills of different specimens. **E.** Frontoclypeus of male pupa. **F.** Same, female pupa. **G.** Platelets of thorax. H–K. Larva. **H.** Antenna. **I.** Terminal sensillum of antenna. **J.** Apex of mandible. **K.** Marginal serrations of mandible. **L.** Distal portion of pupal gill. M, N. Larva. **M.** Teeth of hypostomium. **N.** Teeth of cephalic fan ray.

mm; cephalopterothecal length 3.6–3.7 mm. Position and general structure of gills much as in *arrarteorum,* but secondary branches stouter and more abruptly tapering apically (fig. 105A–D, L). Shape and proportions of frontoclypeus of male and female pupa as shown in figure 105E, F. Platelets verrucose, numerous, forming clusters (fig. 105G). Facial trichomes hairlike. Thorax with platelets and trichomes similar to those of *arrarteorum.* Setae of abdominal tergite I hairlike, length 28–42 μm. Setae of abdominal tergite II stouter and longer (52–61 μm). Tergites III and IV each with 4 + 4 hooks; anterodorsal setae slightly longer than hooks. Length of setae of tergite VII 35–60 μm. Spine combs on tergites VI–VIII mostly interrupted, consisting on tergite VII of 21–26 spines, their length 25–30 μm, as long or twice as long as setae of this segment. Specialized setae of abdominal apex absent. Onchotaxy of abdominal sternites as in *arrarteorum.*

Mature larva. Maximum length 11.2 mm; width of head capsule 1.05 mm. Body shape as usual for the genus; ventral papillae present. Color light purple; pigment most intense on upper surface of posterior portion of body. Head light yellow brown; dark markings very conspicuous. Posterolateral spots of cephalic apotome confluent and more intensive than in *arrarteorum.* Hypostomial bridge darkened, with faint median longitudinal band whitish. Antennae as long as stem of cephalic fan, distinctly pigmented, but third segment not darker than preceding. Shape of antennae as in figure 105H. Ratio of segments I–III =

1:0.7–0.9:1.2–1.3. Terminal antennal segment 3.5–4.0 times as long as wide at base (fig. 105I). Cephalic fan with 27–33 large rays, small teeth very irregular (fig. 105N), only slightly shorter than large teeth. Mandible (fig. 105J, K) with 10–12 inner teeth and 14–17 marginal serrations. Maxillary palp 2.3 times as long as wide at base. Hypostomium (fig. 105M) of same general structure as in *cilicinus* and *arrarteorum,* with 12–15 lateral serrations and 10–12 hypostomial setae arranged in one or two irregular rows. Cervical sclerites much as in *arrarteorum,* but more heavily sclerotized and with membrane connecting oval platelets to transversal sclerites. Lateral sclerite of proleg with about 56 teeth. Gill histoblast and perianal scales as in *arrarteorum.* Recurrent struts well developed, crochet ring with 120–128 rows with 26–28 hooks each.

HOLOTYPE: ECUADOR: *Cotopaxi:* Rio Zumbahua on road Pujili-Quevedo, 3500 m, July 29, Aug. 10, 1969 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, allotype female, one paratype female with pupal exuvia, two pharate females and one male paratype, several pupae and larvae; Tunguruhua, road Ambato-Guaranda, W slope of Chimborazo, 3750 m, Aug. 11, 1969 (P. and B. Wygodzinsky; AMNH).

ETYMOLOGY: The name *clandestinus,* hidden or concealed, is an allusion to the place where the aquatic stages were found; they were very difficult to see because they closely resembled the support to which they were attached.

DISCUSSION: This species is very close to *arrarteorum,* with small differences in size and the proportions of organs, colors, and number of teeth or hooks, as noted in the keys. Together with *bolivianus* and *jatunchuspi, clandestinus* is one of the largest species of *Gigantodax.*

Gigantodax cilicinus, new species
Figures 106A–Q, 107A–K, 108A–K

DIAGNOSIS: *G. cilicinus* differs from the closely related *arrarteorum* and *clandestinus* by the shorter calcipala of the adult and the somewhat differently shaped gills of the pupa, as described, mentioned in the key, and illustrated.

DESCRIPTION: Female unknown.

Male (pharate). Length of wing more than 5.5 mm. Color unknown. Holoptic. Frontoocular triangle very small (fig. 106G). Shape and proportions of antennal segments as in figure 106A; ratio length/width of first flagellomere 1:0.63–0.67. Terminal segment of maxillary palp 1.5 times as long as penultimate (fig. 106B). Sensory vesicle (fig. 106C) suboval, with distinct neck. Sc with 35–38 hairs. R with setae in two or three irregular rows. R_1 with setae in one or two rows; spinules well developed, but not numerous (5–9), irregularly scattered among setae, beginning apicad of level of insertion of Sc and C, in some cases restricted to apical half of R_1. R_s with setae on undersurface basally in one, apically in two or three irregular rows, on upper surface with setae in one row but bare on basal portion. Shape and proportions of fore and hind leg segments as shown in figure 106D, E. Fore basitarsus 11.5–13.4 times, hind basitarsus approximately 6.6–7.1 times as long as wide. Calcipala very short, covering only basal fourth of second tarsomere (fig. 106I). Genitalia as shown in figure 106F, H, J–M; distimere almost as long as basimere, with two or three apical spines.

Pupa. Cocoon small, covering pupa dorsally only to base of abdomen, ventrally to head (fig. 107A). Color of cocoon very light brown, tightly woven but translucent, somewhat parchmentlike. Length of cocoon along dorsum 3.5–4.3 mm, ventrally up to 6.0 mm. Total length of body of pupa 5.5–6.5 mm; cephalopterothecal length 3.2–3.3 mm. Gills light brown, compact, short, with 16 or 17, very rarely 18, secondary branches, wide at base and for most of their length rather abruptly pointed apically and with long respiratory filaments (fig. 107B–D). Branches completely covered with long hairlike cuticular processes (Fig. 107C). All branches situated in the same plane, this plane inclined in relation to longitudinal axis of body of pupa; general shape of gill highly irregular. Secondary branches extremely varied in size; in most specimens second to fifth branches arising consecutively from common trunk, sixth and seventh very short, arising together from elongate primary branch. Shape and propor-

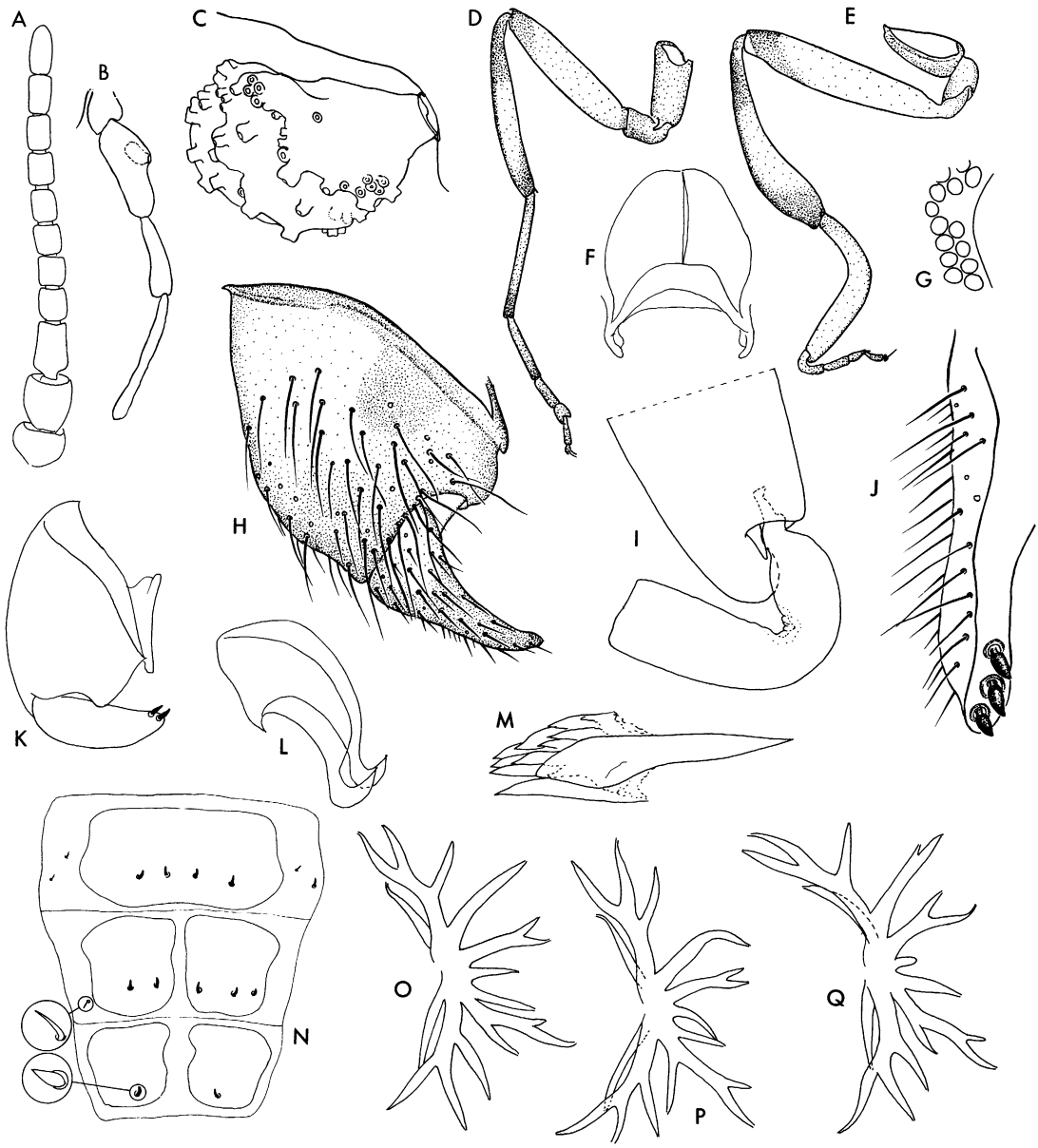

Fig. 106. *Gigantodax cilicinus.* **A–M.** Male. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle of maxillary palp. **D.** Foreleg. **E.** Hind leg. **F.** Ventral plate. **G.** Fronto-ocular triangle. **H.** Basimere and distimere. **I.** Calcipala, with second tarsal segment. **J.** Distimere, under surface. **K.** Basimere and distimere. **L.** Median sclerite, sublateral aspect. **M.** Endoparameral organ. **N.** Sternites V–VII. **O–Q.** Gills.

tions of frontoclypeus of female and male pupa as shown in figure 107E, J; platelets glabrous, most numerous along borders, less so on disc (fig. 107E, K). Facial trichomes as shown in figure 107H. Thorax with platelets glabrous, arranged much as on clypeus. Dorsocentral and dorsolateral trichomes very short, delicate, hairlike (fig. 107F). Setae of abdominal tergite I (fig. 107G) extremely short (18–22 μm) and delicate; setae of tergite II stouter and much longer (50–60 μm). Tergites III and IV each with 5 + 5 short hooks, the

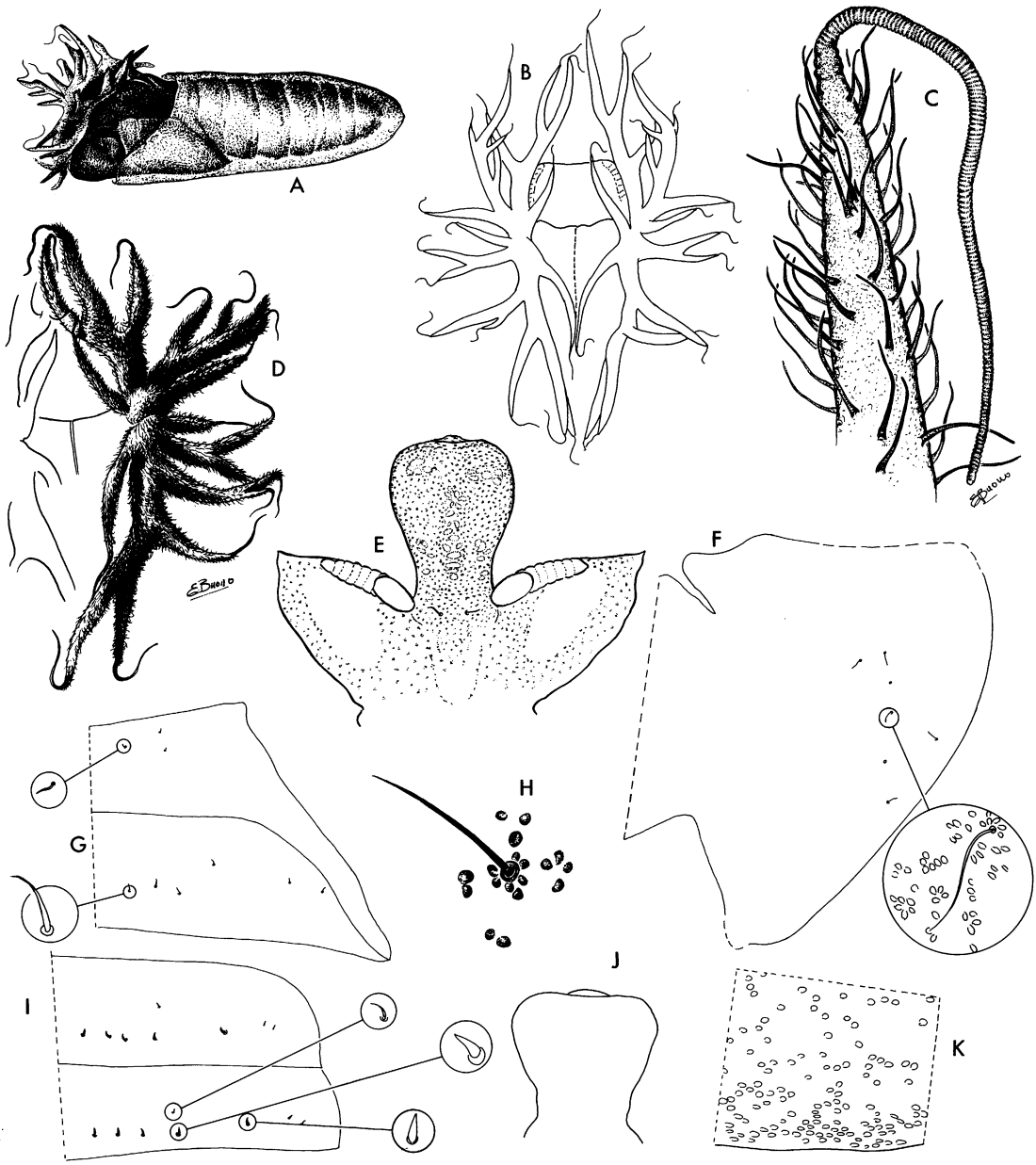

Fig. 107. *G. cilicinus.* Pupa. **A.** Pupa in cocoon, side view. **B.** Frontal view. **C.** Apex of gill branch, with respiratory filament. **D.** Gill. **E.** Part of head capsule of male. **F.** Portion of thorax, with trichomes. **G.** First and second abdominal tergite. **H.** Facial trichome. **I.** Third and fourth tergite. **J.** Outline of frontoclypeus, female. **K.** Platelets of clypeus.

outermost ones remote from the 4 + 4 remaining ones (fig. 107I), in some cases also somewhat more slender. Anterodorsal setae very small as compared to hooks. Setae of tergites V–VIII slender, minute; length of tergite VII 22–23 μm. Spine-combs on tergites VI–VIII continuous or interrupted at middle, unusually short, consisting on tergite VII of 16–19 spines, their length 10–12 μm. Specialized setae of eighth and ninth segments

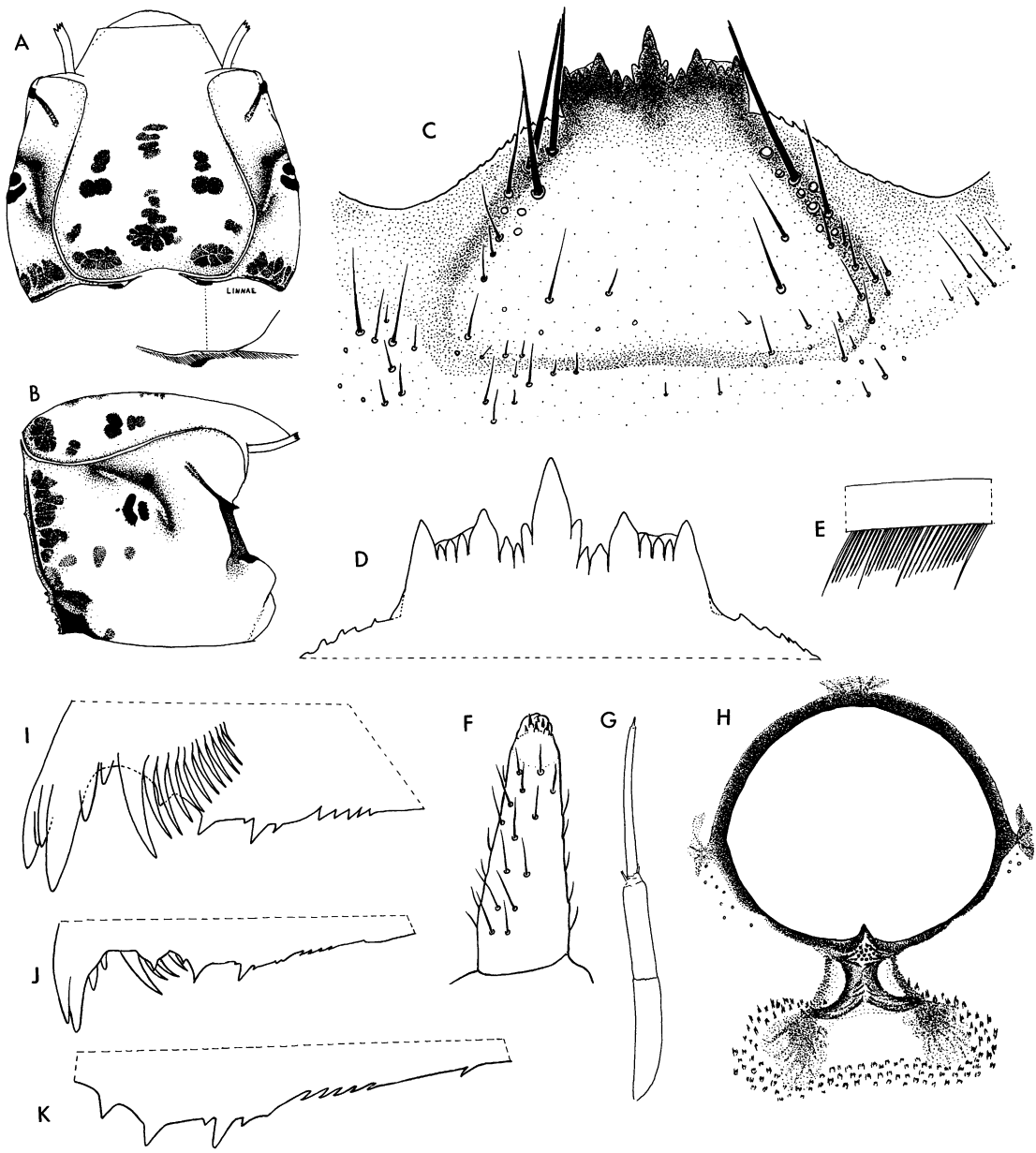

Fig. 108. *G. cilicinus.* Larva. **A.** Head, dorsal aspect. **B.** Head, side view. **C.** Hypostomium. **D.** Apical portion of hypostomium. **E.** Teeth of ray of cephalic fan. **F.** Maxillary palp. **G.** Antenna. **H.** Anal sclerite. **I, J.** Apex of mandible. **K.** Mandibular serrations.

absent, or reduced to a few fine, inconspicuous hairs. Sternite IV with short setae. Sternite V with only 2 + 2 sternal plates, VI with 2 + 2, VII with 1 + 1 short hooks; pleural membranes of segment V and in some cases VI with one or two stout but not hooklike setae. Sternite VIII glabrous.

Mature larvae. Length 13–14 mm; width of head capsule 0.11 mm. Body shape as usual for genus; ventral papillae small but distinct. Color of larva whitish, with faint overall hypodermal pigment. Head light yellow; spots of cephalic apotome very distinct; posterolateral spots completely separated, dis-

tance between spots larger than their transversal diameter (fig. 108A). Distribution of pigment on sides of head as in figure 108B. Hypostomial bridge darkened, with faint median longitudinal band whitish. Antenna as long as stem of cephalic fans, distinctly although not strongly pigmented, third segment not darker than preceding. Shape of antenna as in figure 108G; ratio of segments I–III = 1:0.7–0.9:1.1–1.2. Teeth of cephalic fan as shown in figure 108E. Terminal sensillum about 3.5–4 times as long as wide. Mandible with 10–11 inner teeth and 12–16 marginal serrations (fig. 108I–K). Maxillary palp 2.5 times as long as wide at base (fig. 108F). Hypostomium as shown in figure 108D. Median tooth projecting considerably beyond level of apices of corner teeth; imaginary line connecting apex of median tooth to apex of fourth lateral tooth not intersecting any other tooth; corner teeth projecting beyond level of apex of first intermediate teeth. Hypostomium with 7–9 lateral serrations and 10–12 hypostomial setae arranged in two irregular rows. Cervical sclerites consisting of 1 + 1 heavily sclerotized platelets fused to narrow, transverse, sclerotized bands (fig. 108A). Gill histoblast as illustrated for *arrarteorum.* Recurrent strut very well developed. Perianal scales well developed, numerous, forming complete circumanal ring (fig. 108H). Crochet ring with 150–200 rows of 27–29 hooks each.

HOLOTYPE: ARGENTINA: *San Juan:* International highway, about 10 km from Chilean border, 3500 m, Nov. 7, 1967 (S. Coscarón; MLP), pharate male with associated pupal exuviae.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 pharate male with associated pupal exuviae, paratype (AMNH), pupae, and larvae. BOLIVIA: *La Paz:* road from La Paz to La Cumbre, about 4000 m, Oct. 27, 1968 (S. Coscarón; AMNH), 1 pupa, 1 larva; ibid., 4400 m (S. Coscarón; AMNH), 1 pupa, larvae; road from La Paz to the Yungas de Coroico, east slope of mountain range, between 3600 and 4500 m, Oct. 29, 1968 (S. Coscarón; MLP), larvae.

ETYMOLOGY: The specific name is taken from the Latin *cilicinus,* make of hair cloth, a reference to the texture of the gills of the pupa.

BIOLOGY: The aquatic stages of this high mountain species were found on the undersides of stones in small, slow flowing creeks with clear, cold water (10°C), together with larvae of *Simulium* (*Pternaspatha*) sp.

DISCUSSION: The above description is based on material from San Juan, Argentina. The specimens from La Paz, Bolivia, are at this time listed under *cilicinus,* with which they are either identical or to which they are very closely related. Only larvae and two pupae were available from the Bolivian populations. We have been unable to find differences in the larvae; in the pupae we observed that the stem bearing gill branches 6 and 7 are much shorter than in *cilicinus* from San Juan. Future research, based on more complete material, will contribute toward deciding the taxonomic status of the Bolivian populations.

Gigantodax cilicinus, as well as *arrarteorum* and *clandestinus,* differs from all known *Gigantodax* species by the combination of the structure of the larval hypostomium, with its strongly projecting median tooth, and the peculiar gill of the pupa. The presence of a very small fronto-ocular triangle in the male, and the virtual absence of specialized setae on the terminal segments of the abdomen of the pupa are likewise unique in the genus.

The most peculiar characters of *cilicinus* are the often reduced number of gill branches in the pupa, hooks on abdominal sternite V, and the increased number of hooks on tergites III and IV to 5 + 5. Because of these autapomorphies, we consider this species as the most derived member of the *cilicinus* group.

cormonsi group

DIAGNOSIS: Recognized by the pupal gill with 18 branches with cuticular processes, often fused, making a shield, and branches 12 and 16 longer than the others; subbasal tooth of claw in females subtriangular, median hypostomium tooth below level of corner teeth, and recurrent struts only locally pigmented.

Female. Medium to large reddish brown species. Morphology very close to *brophyi* group. Subbasal tooth of claw subtriangular (figs. 123G, 126Q, 178D) (except subtrapezoidal in *misitu,* fig. 112J); R_1 with spinules.

Male. Morphology similar to that of *brophyi* group.

Pupa. Cocoon generally well developed with 18 tubular, hairy, cuticular processes and caducous filaments distally; gill branches mostly fused, making a shield, but distinct, 12th and 16th elongated (figs. 120B, 122A, 127D, F). Trichomes of frontoclypeus and thorax not apically hooked, the facial and dorsocentral trichomes spinelike (except *abalosi*). Distal segment with specialized setae from straight to curved or twisted. Abdominal tergite I with 4–7 + 4–7 trichomes, with sublateral ones often more stout than others.

Larva. Cephalic apotome widest near base. Antenna reaching or past level of stem of cephalic fan's apex. Terminal sensillum comparatively elongated (ratio length/width = 4.0–5.5). Second antennal segment one-half length of basal segment or slightly shorter. Mandible with regular marginal serrations (6–10). Median hypostomial teeth below level of corner teeth. Recurrent struts not well developed, only locally pigmented. Ring of scales complete or not.

DISTRIBUTION: From Venezuela to north of Chile (fig. 137).

DISCUSSION: This is a homogeneous group with 10 species that closely resemble one another. By studying the gill morphology it is possible to see a transformation from incipient fusion of gill branches in *gracilis* (fig. 111A, I) to well fused in *siberianus* (figs. 135B–F, 136J). It is possible to identify pairs of sister species: *gracilis-misitu, brevis-wygodzinskyi, leonorum-abalosi, cormonsi-praealtus,* that, with *vulcanius-siberianum,* compose this group.

Gigantodax gracilis, new species
Figures 110A–Y, 111A–K

DIAGNOSIS: The structure of the fanlike gills of the pupa with the peglike processes on the base of the branches is sufficient to distinguish this species from all others in the genus.

DESCRIPTION: *Female.* Length of wing 4.8–5.1 mm. Head dark gray, its pilosity silver colored. Antenna dark grayish brown; scapus and pedicellus annulated with orange, base of first flagellomere also orange. Maxillary palp piceous. Scutum, scutellum, metanotum, and pleural region light reddish brown; scutum with delicate whitish line longitudinally along middle. Pilosity of thorax from silver to brass colored. Wing translucent; veins light yellow. Setae on stem vein piceous, tinged with reddish; remaining wing setae dark. Halter very light brown. Legs yellowish brown, not conspicuously pigmented; setae concolorous. Abdominal tergites dark brown, with hind margins yellowish white; last four or five segments also with disc of tergite mottled to varied in extent of light color. Abdominal hairs light brass colored.

Frontal angle 50°. Fronto-ocular triangle about as high as wide (fig. 110B). Shape and proportions of antennal segments as shown in figure 110A. Mandible with 16–20 teeth, the last five obsolescent, and only the first four or five well developed, the remaining comparatively small (fig. 110C). Maxilla with 20–22 teeth. Last segment of maxillary palp almost twice as long as penultimate (fig 110E). Second segment of maxillary palp broadly oval, ratio length/width 1:0.57–0.59. Sensory vesicle comparatively small (fig. 110D) with very short neck. Sc with 23–26 hairs. Setae on R and R_1 arranged in one or two irregular rows. Spinules on R_1 beginning at or apical to level of insertion of Sc on C, well developed but much less numerous than setae. Setae on concave portion of R_s in two to three rows, on upper (convex) section in one row. A_2 not reaching wing margin. Shape and proportions of leg segments as in figure 110F, G. Hind basitarsus 6.9–7.4 times as long as wide. Calcipala surpassing middle of second tarsomere (fig. 110J). Basal tooth of claw subtriangular (fig. 110H). Abdominal sternites with only delicate hairs, genitalia without special characters.

Male. Length of wings 4.6 mm. Color as in female, but scutum darker reddish brown, and only disc of last three abdominal tergites mottled with light color.

Holoptic. Shape and proportions of antennal segments as shown in figure 110L; ratio length/width of first flagellomere 1:0.56–0.59. Apical segment of maxillary palp distinctly longer than penultimate (fig. 110L). Sensory vesicle (fig. 110M) small, subglobular, with very short neck. Wing as in female. Shape and proportions of foreleg segments as in figure 110S. Fore basitarsus 13.0–13.7 times as long as wide, hind basitarsus 6.35 times as

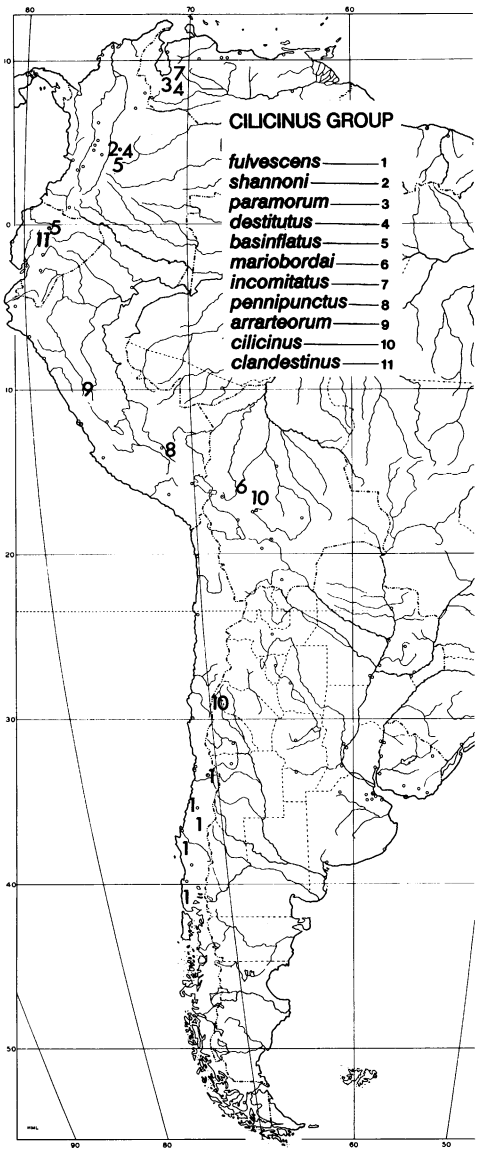

Fig. 109. Map with the distribution of species of *cilicinus* group.

long as wide (fig. 110O). Calcipala surpassing middle of second tarsomere (fig. 110K). Genitalia without special characters. Distimere approximately two-thirds as long as basimere, with two apical spines (fig. 110I). Main body of ventral plate as long as wide.

Pupa. Cocoon large, covering entire body of pupa, leaving only gills exposed. Cocoon translucent, light brown, not very tightly woven, individual strands easily perceptible. Length of cocoon along dorsum 4.6–5.4 mm. Total length of body of pupa 4.3–4.5 mm; cephalopterothecal length 2.5–2.7 mm. Gill with 18 branches, forming a fanlike, forward-facing structure (figs. 111A, C, I). All branches stout at base, becoming progressively more narrow beyond basal portion, filiform apically. Basal portion of all branches with short toothlike or peglike cuticular processes (fig. 111A, B), in all cases shorter than diameter of branch; remaining portion of branches glabrous, minutely dotted. Gill branches subequal in length, some fused closely to their base, some arising by twos and threes from very short common trunks. First dorsal branch single; second and third arising from well-developed common trunk. Fourth, fifth, and sixth, in some cases also seventh, fused at their bases; areas of contact of branches marked by line of small perforations. Seventh and eighth, ninth, and tenth branches arising as pairs from very short common trunks; 11th to 14th arising from short but distinct common branch; 11th and 14th on each side at base, 12th and 13th apically on common trunk; 15th to 17th inserted on common trunk; 18th branch single. Shape and proportion of frontoclypeus of male and female as in figure 111H, K; surface of frontoclypeus with irregular rugosity; platelets absent. Facial trichomes slender, spinelike. Platelets on dorsal portion of thorax weakly defined, smooth, not numerous, scattered or forming poorly defined groups (fig. 111J). Dorsocentral trichomes slender, spinelike; dorsolaterals very delicately hairlike (fig. 111D). Setae of first and second abdominal tergites hairlike, those of first tergite slightly shorter (50–65 μm) than those of second tergite (60–70 μm) (fig. 111E). Tergites III and IV each with 4 + 4 short hooks (fig. 111G). Anterosublateral setae hairlike (fig. 111F). Setae of tergites V–VIII slender, their length on tergite VII about 100 μm. Spine-combs on tergites VI–VIII continuous, consisting on tergite VII of 21–37 spines, their length 25–30 μm, viz., from one-fourth to one-third as long as setae of this tergite. Specialized setae of segments VIII and IX straight, curved, or hooked, rarely branched. Sternite V with 3 + 3, VI with

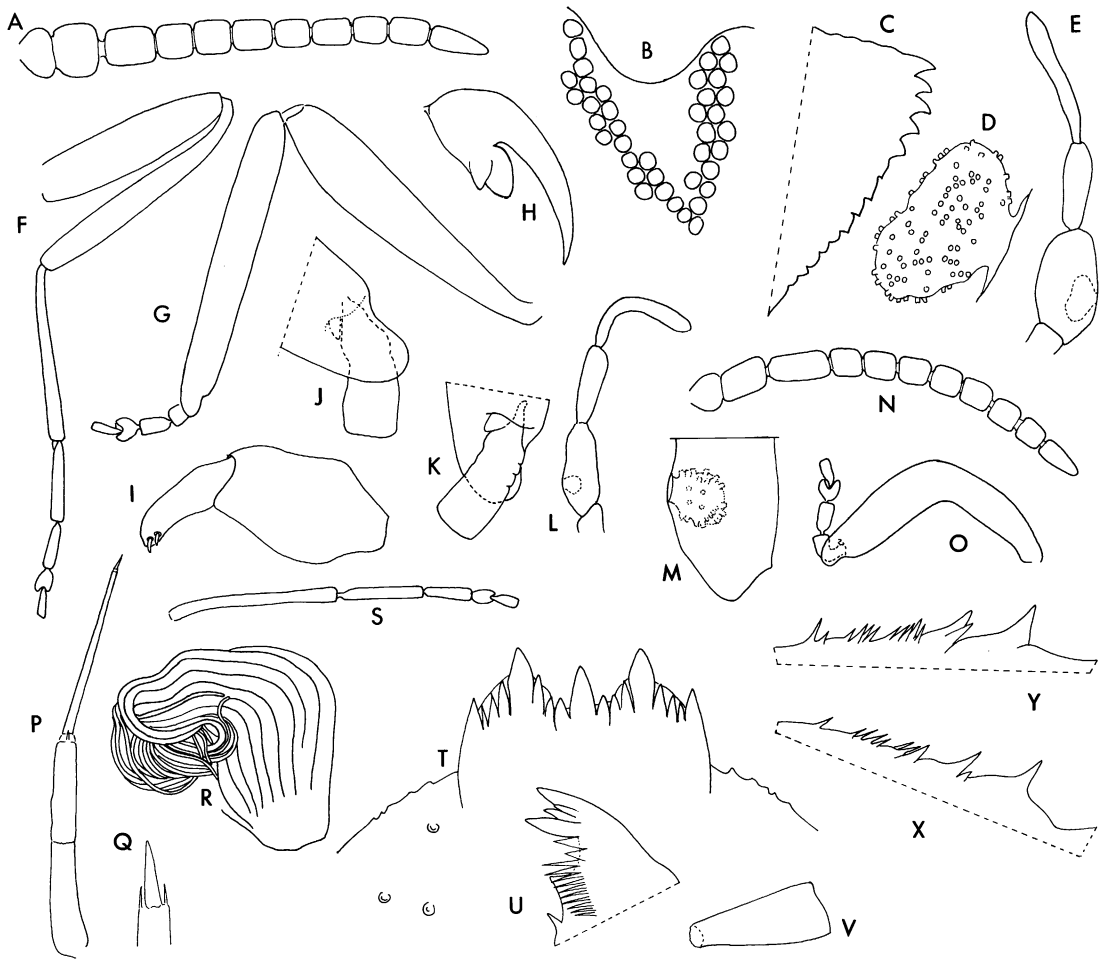

Fig. 110. *Gigantodax gracilis.* A–H. Female. **A.** Antenna. **B.** Fronto-ocular triangle. **C.** Apex of mandible. **D.** Sensory vesicle of maxillary palp. **E.** Maxillary palp. **F.** Foreleg. **G.** Hind leg. **H.** Claw. **I.** Basimere and distimere. **J.** Calcipala of female. **K.** Same, male. L–O. Male. **L.** Maxillary palp. **M.** Portion of second maxillary palp, with sensory vesicle. **N.** Antenna. **O.** Posterior tarsus. **P.** Antenna of larva. **Q.** Apical sensillum of antenna of larva. **R.** Gill histoblast. **S.** Foreleg of male. **T.** Hypostomium. **U.** Apex of mandible of larva. **V.** Maxillary palp of larva. **X, Y.** Lateral serrations of mandible.

2 + 2, and VII with 1 + 1 hook; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 8.3–8.5 mm; width of head capsule 0.75–0.8 mm. Body shape as usual for the genus; ventral papillae well developed. Color of larva whitish. Head whitish; spots of cephalic apotome faint. Hypostomial bridge lacking pigment. Antenna about as long as stem of cephalic fan, pigment very faint. Shape of antenna as in figure 110P; ratio of segments I–III = 1:0.75–0.8:1.30. Terminal sensillum three to four times as long as wide at base (fig. 110Q). Cephalic fan with 30–31 large rays. Small teeth rather uniform in size. Mandible (fig. 110U, X, Y) with nine inner teeth and 11–12 marginal serrations. Maxillary palp 2.2 times as long as wide at base (fig. 110V). Hypostomium (fig. 110T) with median tooth falling considerably short of level of third intermediate tooth apex; line connecting apex of corner tooth with apex of fourth lateral tooth meeting at 90°. Hypostomium with six to seven marginal serrations

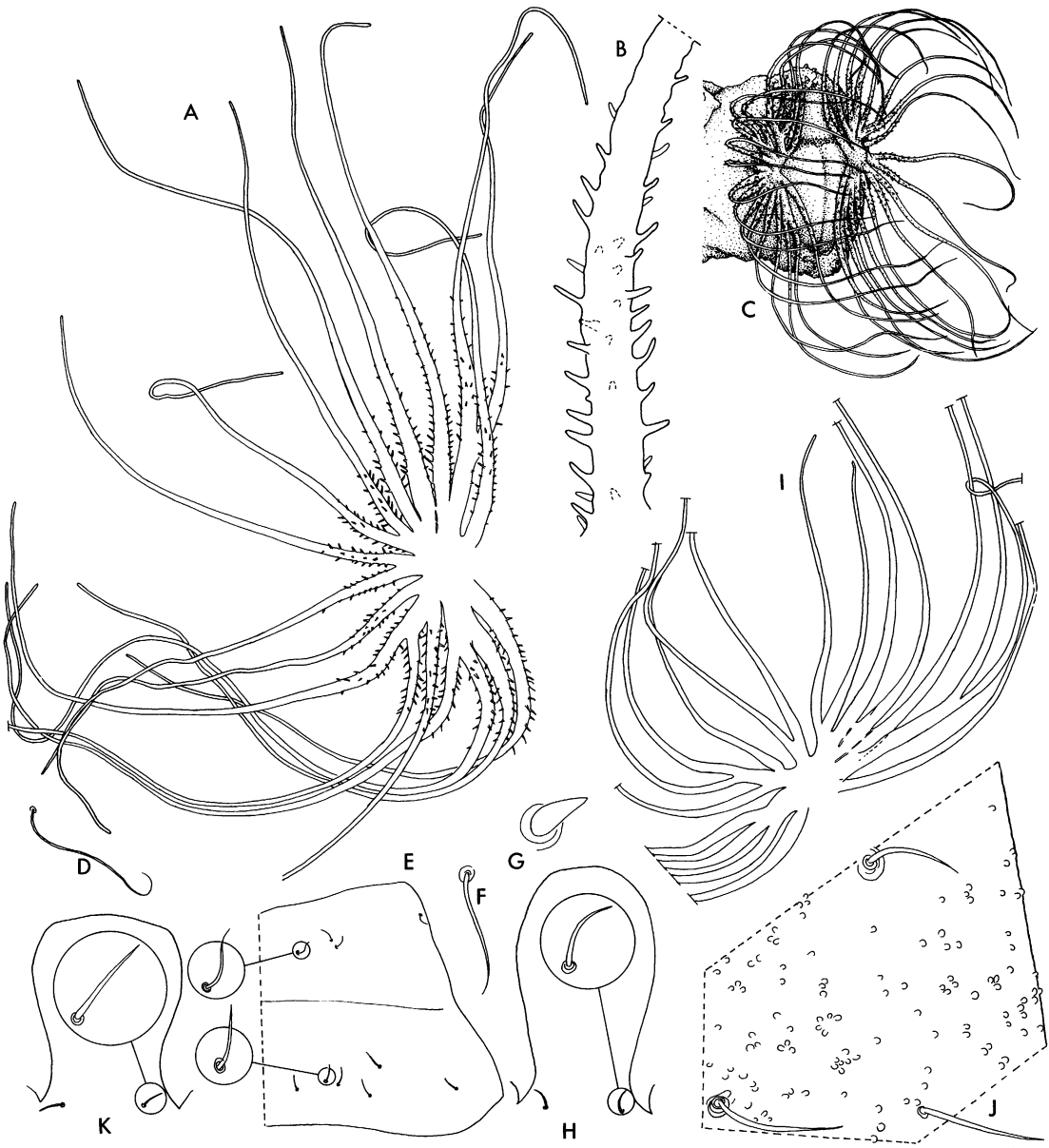

Fig. 111. *G. gracilis.* Pupa. **A.** Gill. **B.** Detail of basal portion of gill branch. **C.** Anterior portion of body of pupa with gills, oblique view. **D.** Trichome dorsolateral of thorax. **E.** Chaetotaxy of abdominal tergites I and II. **F.** Anterosublateral trichome of abdominal tergite III. **G.** Hook of tergite IV. **H.** Frontoclypeus of male. **I.** Gill. **J.** Detail of thorax, with platelets and trichomes. **K.** Frontoclypeus of female.

and two or three hypostomial setae in each row. Cervical sclerites as in *G. cormonsi.* Gill histoblast as in figure 110R; extreme base orange colored, remainder blackish. Perianal scales forming 1 + 1 conspicuous patches at base of upper arms of X-shaped sclerite, consisting of large, heavily pigmented scales; other very small and faintly pigmented scales

forming complete although tenuous circumanal ring. Recurrent struts of anal sclerite very lightly pigmented, difficult to perceive. Crochet ring with about 75 rows consisting of 15 hooks each. Rectal gills not examined.

HOLOTYPE: ECUADOR: *Pichincha:* road Quito-Papallacta, 3300 m, July 24–Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype: 1 female, allotype, 1 male, 5 females, paratypes (all reared, and with associated pupal exuviae), pupae, and larvae. ECUADOR: *Pichincha:* Amaguana, 2650 m, Aug. 13, 1969 (P. and B. Wygodzinsky; AMNH), 1 pupa. *Cotopaxi:* 10 km N of Latacunga, 3100 m, July 26, 1969 (P. and B. Wygodzinsky; AMNH), 1 larva.

ETYMOLOGY: The specific name is from the Latin *gracilis*—delicate, slender—referring to the delicate branches of the gill of the pupa.

BIOLOGY: The aquatic instars of *G. gracilis* were collected in small, clear streams or in irrigation ditches not more than 2 ft wide; the pupae occurred on the undersurfaces of stones, together with those of other species of the genus.

DISCUSSION: The basic structure of the gills of the pupa suggests affinity of this species with *brevis* and *wygodzinskyi,* and others of the *cormonsi* group (sensu lato). The gills, which form a fanlike, forward-facing structure, are not unlike those of the species mentioned, as are the fusions near their bases of a certain number of the dorsalmost branches, and of course, the presence of spinelike cuticular processes on the branches. The fact that all 18 branches are of approximately identical length, and that the amount of basal fusion of the branches is very limited, suggests that *gracilis* has plesiomorphic gills within the group under consideration. The somewhat irregularly developed teeth of the female mandibles and the very weak recurrent struts of the anal armature of the larva are notable autapomorphic characters.

Gigantodax misitu, new species
Figures 112A–S, 113A–J, 114A–P

DIAGNOSIS: Differs from all other species of the genus by the structure of the gills of the pupa, by having 18 branches covered with spinelike hairs and arranged into a subsemicircular structure perpendicular to the longitudinal axis of the body, with branches 12 and 16 longer than the remaining ones and with respiratory filament near the base of the branch.

DESCRIPTION: *Female.* Length of wing, 5.0–5.2 mm. Color as in *cormonsi,* with scutellum as dark as metanotum. Frontal angle 35–40°. Fronto-ocular triangle slightly higher than wide (fig. 112G). Shape and proportion of antennal segments as shown in figure 112L. Mandible with 22–25 teeth. Terminal segment of maxillary palp slightly longer than penultimate (fig. 112M). Second segment of maxillary palp elongate, apical half narrowed, ratio length/width = 1:0.43–0.49. Sensory vesicle large, with distinct neck (fig. 112N). Maxilla with 24–26 teeth. Sc with 34–35 hairs. R with setae arranged in one or two irregular rows. R_1 with setae in two rows; spinules present, beginning basal to level of insertion of Sc on C. R_s with setae arranged in two irregular rows. A_1 almost reaching wing margin. Shape and proportions of fore and hind leg segments as in figure 112D, E. Hind basitarsus 6.9–7.3 times as long as wide. Calcipala distinctly surpassing middle of second tarsomere (fig. 112I). Basal tooth of claw as shown in figure 112J. Eighth abdominal sterna with only delicate hairs. Genitalia without special features. Genital fork, spermatheca, cercus, and paraproct as in figure 112F, K, R.

Male. Length of wing 4.6–4.8 mm. Color as in female, but scutum dark reddish brown tinged with piceous, as scutellum and metanotum.

Holoptic. Shape and proportion of antennal segments as in figure 112A; ratio of length/width of first flagellomere 1:0.53–0.59. Maxillary palp as in figure 112B, sensory vesicle small, suboval, with distinct neck (fig. 112C); Sc with 10–18 setae, leaving apical portion of vein bare. R and basal portion of R_1 and R_s with setae only in one row; spinules of R_1 as in female. R_1 on apical portion with setae in two irregular rows. A_2 almost reaching wing margin. Shape and proportions of fore and hind leg segments as in figure 112P, Q. Fore basitarsus 14.5–16.5 times as long as wide; hind basitarsus 5.85–6.50 times as long as

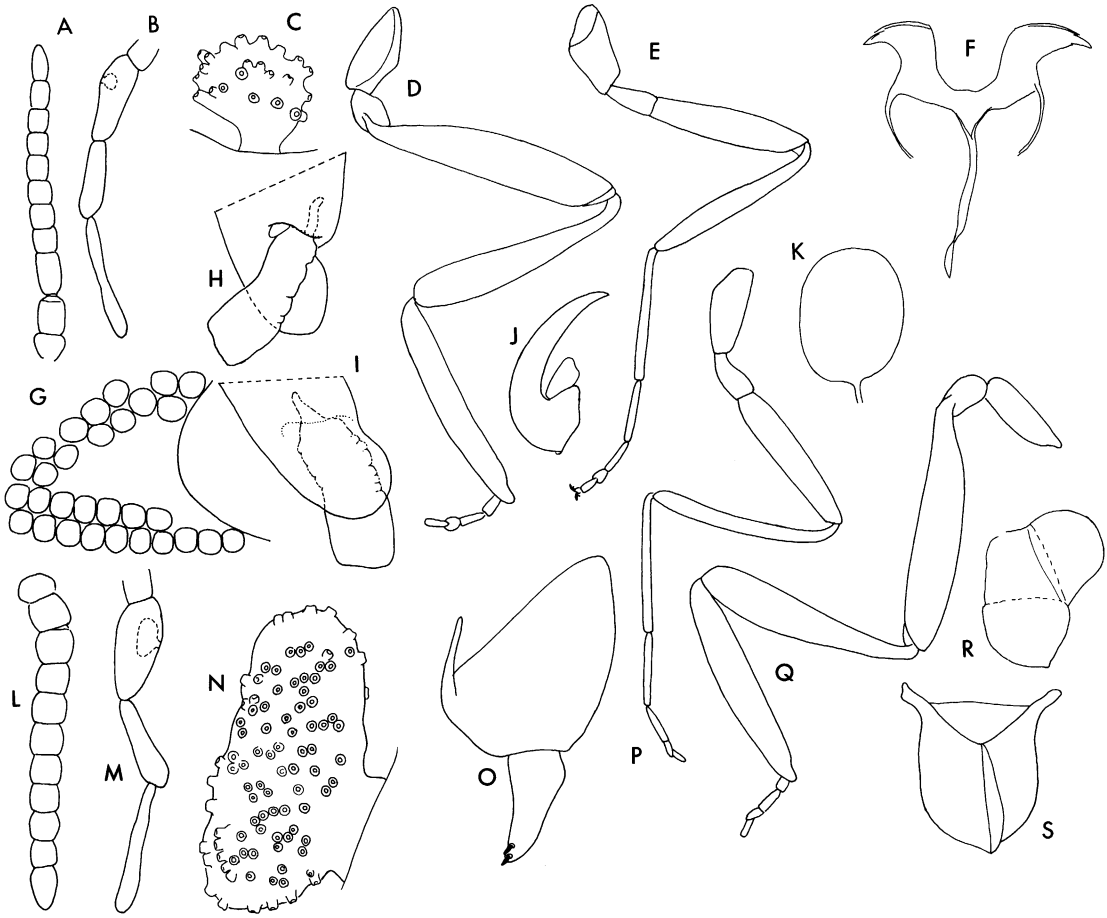

Fig. 112. *Gigantodax misitu.* A–C. Male. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle of maxillary palp. D–G. Female. **D.** Hind leg. **E.** Foreleg. **F.** Genital fork. **G.** Fronto-ocular triangle. **H.** Calcipala, with second tarsal segment. I–N. Female. **I.** Calcipala. **J.** Claw. **K.** Outline of spermatheca. **L.** Antenna. **M.** Maxillary palp. **N.** Sensory vesicle of maxillary palp. **O.** Basimere and distimere. P–Q. Male. **P.** Foreleg. **Q.** Hind leg. **R.** Cercus and paraproct. **S.** Basal plate.

wide. Calcipala (fig. 112H) surpassing middle of second tarsomere. Distimere more than two-thirds as long as basimere, with two apical spines (fig. 112O). Main body of ventral plate as long as wide (fig. 112S).

Pupa. Cocoon irregularly wall-pocket shaped, large, completely covering body of pupa except head and gills (fig. 113B–D). Color of cocoon light brown, tightly woven but translucent; anterior border slightly but perceptibly thickened. Length of cocoon along dorsum about 7.5 mm. Total length of body of pupa 4.5–5.0 mm; cephalopterothecal length 2.7–3.0 mm. Gills (fig. 113A–G) each with 18 branches in fanlike arrangement; main body of gills perpendicular to longitudinal axis of body of pupa, facing forward. First and second branches very short. Third to 11th, 13th to 15th, and 17th and 18th branches of medium size; 12th and 16th much longer than the others, 16th distinctly thicker than 12th. First to seventh or eighth branches partially fused at their base, lines of fusion indicated by series of irregularly shaped perforations. All branches with numerous, strong, heavily pigmented, spinelike cuticular processes (fig. 113A, G) covering entire branch, except 12th and 16th covered for most of their length by minute, cuticular tubercles (fig. 113F). All branches, except 12th and 16th,

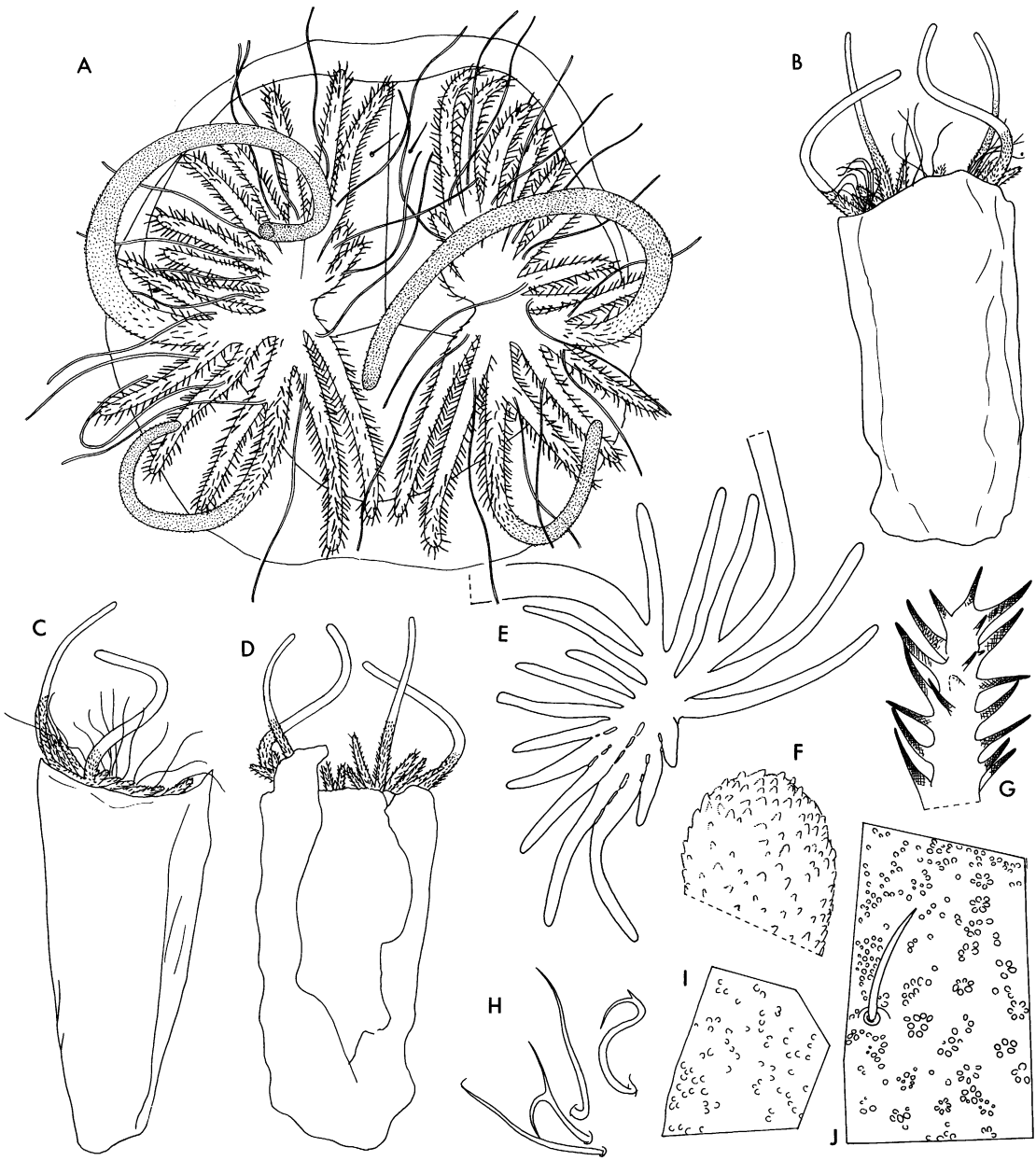

Fig. 113. *G. misitu.* Pupa. **A.** Anterior portion of body with gills, frontal view. B–D. Pupa in cocoon. **B.** Dorsal aspect. **C.** Lateral view. **D.** Under surface. **E.** Gill. **F.** Terminal gill branch. **G.** Terminal portion of short gill branches. **H.** Modified setae of terminal segments of abdomen. **I.** Platelets of clypeus. **J.** Portion of thorax of pupa, with platelets and trichome.

with long respiratory filaments inserted near base of respective branch. Shape and proportions of frontoclypeus of male and female as in figure 114B, E; platelets not numerous (fig. 113I), verrucose. Facial trichomes slender spinelike (fig. 114K). Thorax with platelets heavily verrucose (fig. 114H), scattered or arranged in small, in many cases rosettelike, groups (fig. 114J). Dorsocentral trichomes spinelike, dorsolaterals elongate,

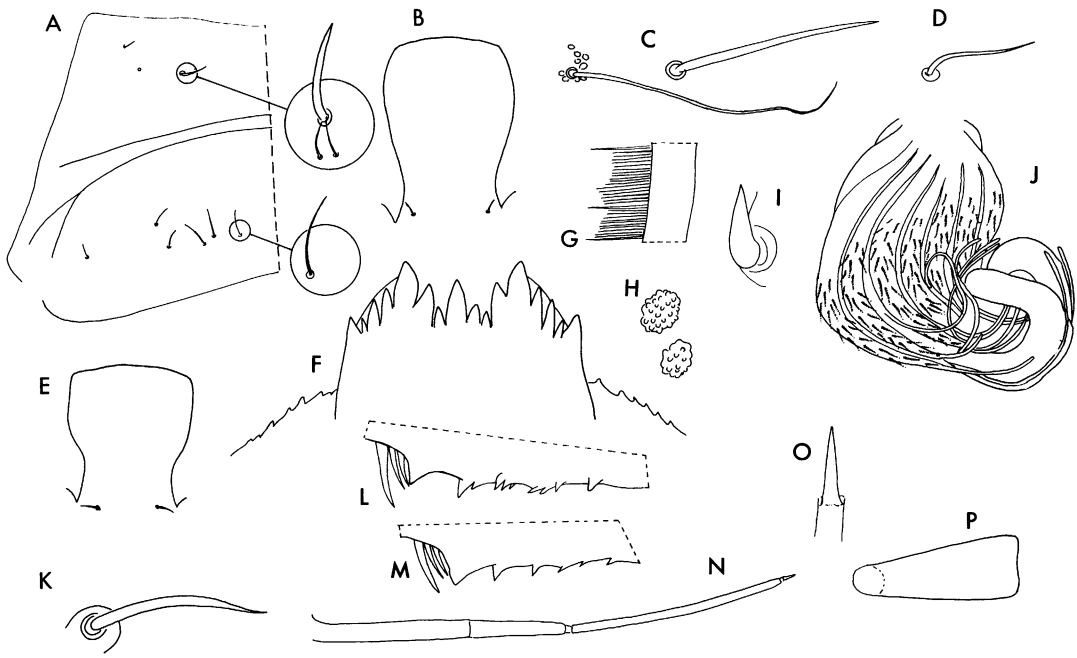

Fig. 114. *G. misitu.* **A.** Chaetotaxy of first and second abdominal tergite. **B.** Frontoclypeus of male. **C.** Dorsocentral above, and dorsolateral below, trichome of abdominal tergite III. **D.** Anterosublateral trichome of thorax of pupa. **E.** Frontoclypeus of female. **F.** Anterior region of hypostomium. **G.** Teeth of rays of cephalic fan. **H.** Platelets of thorax of pupa, high magnification. **I.** Hook of tergite IV of pupa. **J.** Gill histoblast. **K.** Trichome face of pupa. L–P. Larva. **L, M.** Portion of mandibles. **N.** Antenna. **O.** Terminal sensilla of antenna. **P.** Maxillary palp.

hairlike (fig. 114C). Abdominal tergite I with 1 + 1 very strong spines, about 100 μm long (fig. 114A) and a few short hairs (60–80 μm); setae of tergite II 90–100 μm long. Tergites III and IV each with 4 + 4 short hooks (fig. 114I). Anterosublateral setae (fig. 114D) hairlike, setae of tergites V–VIII very slender, their length on tergite VII 85–95 μm. Spinecombs on tergites VI–VIII, continuous, consisting on tergite VII of 35–39 spines, their length 35–40 μm, viz., about one-third the length of setae of this tergite. Specialized setae of eighth and ninth segments irregularly shaped (fig. 113H), in some cases strongly curved, hooked, or branched. Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 8.5 mm. Width of head capsule 0.8 mm. Body shape as usual for genus; ventral papillae well developed. Color of larva whitish, faintly darker on posterior swollen portion of body. Head very light yellow. Spots of cephalic apotome faint; hypostomial bridge lacking pattern elements. Antenna distinctly beyond level of apex of cephalic fan stem, faintly pigmented, third segment slightly but distinctly darker than preceding. Shape of antenna as in figure 114N, unusually slender, first and second segments combined 16 times as long as width of second segment; ratio of segments I–III = 1:0.50–0.54:1.23–1.26. Terminal sensillum approximately five times as long as wide at base (fig. 114O). Cephalic fan with 20–23 large rays, their teeth as shown in figure 114G. Mandibles with 10–12 inner teeth and 9–11 marginal serrations (fig. 114L, M). Maxillary palp slender, about three times as long as wide (fig. 114P). Hypostomium with apex of median tooth falling considerably short of level of corner tooth apex, but reaching or slightly beyond level of third intermediate tooth apex (fig. 114F). Line connecting apex of median tooth to apex of fourth lateral tooth intersecting several teeth between them. Hyposto-

mium with 9–11 lateral serrations and four to five hypostomial setae in each row. Cervical sclerites as in *cormonsi.* Gill histoblast as in figure 114J; basal portion not covered by cuticular processes, orange colored, remaining portion blackish. Perianal scales numerous, strong, and darkly pigmented at level of upper arms of X-shaped sclerite, much less numerous and smaller, less pigmented elsewhere, forming complete though inconspicuous circumanal ring. Crochet ring with 90–100 rows of 18–20 hooks each.

HOLOTYPE: ECUADOR: *Cotopaxi:* NW slope of Mt. Cotopaxi, 3500 m, July 26–Aug. 5, 1969 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female allotype, 24 males, 38 females, paratypes (all reared, and with their associated pupal exuviae), pupae, and larvae. ECUADOR: *Cotopaxi:* road from Quito to Papallacta, 3300 m, July 20–Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), 1 female, paratype (reared, and with associated pupal exuvia), pupae; San Juan, Paramo de Guamani, on Quito-Papallacta road, 3700 m, Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), 1 male, paratype (reared, and with associated pupal exuvia). *Carchi:* Paramo El Angel, Oct. 1969 (C. H. Perez; AMNH), pupae. COLOMBIA: *Cauca:* road from Popayan to Paramo de Purace, 3300 m, Aug. 17, 1967 (P. and B. Wygodzinsky; AMNH), 1 pupa. *Cundinamarca:* road from Bogota to Chonchi, 3100 m, July 13, 1967 (P. and B. Wygodzinsky; AMNH), 1 male, reared, and with its pupal skin; ibid., 3250 m, July 17, 1967 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal exuviae), pupae; ibid., paramo, 3300 m, July 13, 1967 (P. and B. Wygodzinsky; AMNH), one pupa.

ETYMOLOGY: The specific name is taken from *misitu,* Quechua for cat.

BIOLOGY: The pupae of this species were most numerous in small streams or irrigation ditches, at altitudes of 3300–3500 m, and at water temperatures of 9–10°C. Although occasionally found on the undersides of rocks on the bottom of the watercourses, pupae were most numerous on trailing blades of grass and especially on the undersides of watercress leaves; in both cases, pupae were found singly or loosely associated with other pupae of the same or other species of *Gigantodax.*

DISCUSSION: To judge from the structure of the gills of the pupa, *G. misitu* may share a recent common ancestor with *G. wygodzinskyi* and *brevis,* in which both often have fusion of the first upper seven or eight gill branches, and also have the 12th and 16th branches much longer than any of the remaining, which are characters that we saw also in *shannoni* and *destitutus.* The 1 + 1 strong spines of abdominal tergite I of the pupae are equally shared by the three species in question, which also may indicate a recent common ancestry.

Gigantodax brevis, new species
Figures 115A–M, 116A–G, 117A–K

DIAGNOSIS: Differs from *wygodzinskyi,* the most closely related species, by the 11th branch of the pupal gill being broadly rounded apically; the 12th and 16th branches not over twice as long and with distinct, elongate, hairlike, cuticular projections occurring all the way to the base of the respiratory filament.

DESCRIPTION: *Female.* Length of wing 4.3–4.9 mm (average 4.5 mm). Color as in *wygodzinskyi.* Frontal angle 30–35°. Frontoocular triangle higher than wide (fig. 115B). Shape and proportions of antennal segments as in figure 115A. Mandible with 23–26 teeth along only inner margin; subapical portion of outer margin slightly but distinctly serrate. Maxilla with 21–23 teeth. Last segment of maxillary palp slightly longer than penultimate (fig. 115D). Second segment of maxillary palp from suboval to somewhat narrowed apically (fig. 115D, E), ratio length/width = 1:0.44–0.5. Sensory vesicle large, with very short neck (fig. 115C). Sc with 29–32 hairs. R with setae arranged in two or three irregular rows. R_1 with one or two irregular rows of setae, interspersed with numerous spinules beginning at or basal to, level of insertion of Sc on C. R_s with setae in three irregular rows (fig. 115G). A_1 almost reaching wing margin. Shape and proportions of leg segments much as in *wygodzinskyi*; hind leg as in figure 115H; basitarsus 7.2–7.9 times as long as wide. Calcipala distinctly beyond middle of second tarsomere (fig. 115K). Basal

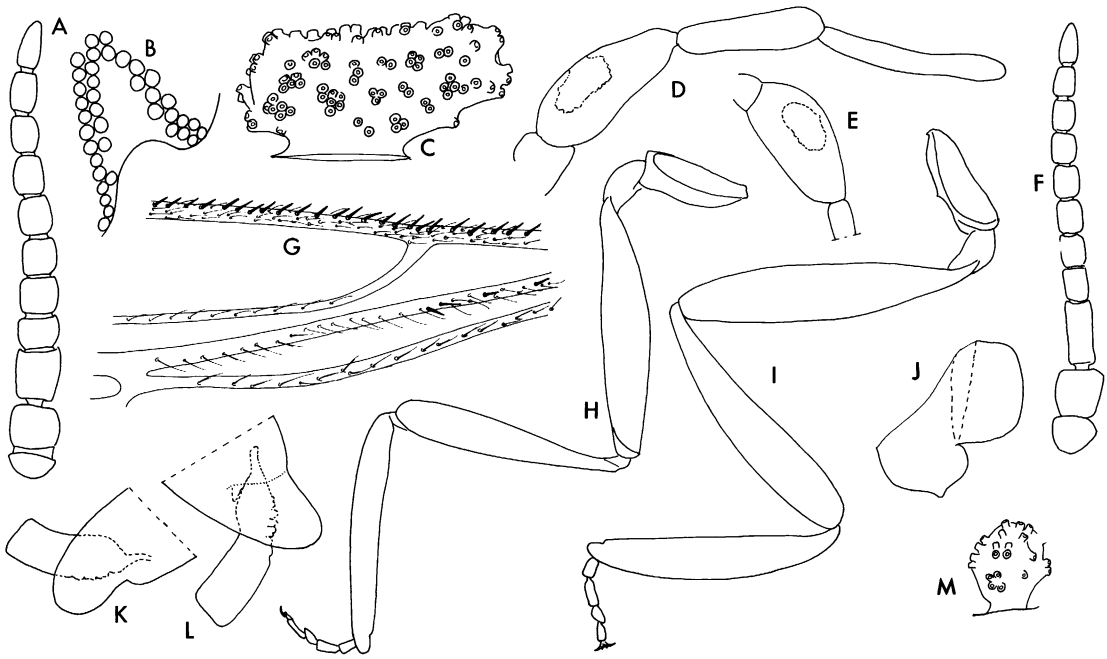

Fig. 115. *Gigantodax brevis.* **A.** Antenna of female. **B.** Fronto-ocular triangle. **C.** Sensory vesicle of maxillary palp of female. **D.** Maxillary palp of female. **E.** Second article of maxillary palp of female. **F.** Antenna of male. **G.** Portion of wing. **H.** Hind leg of female. **I.** Hind leg of male. **J.** Cercus and paraproct. **K.** Calcipala of female, with second tarsal segment. **L.** Same, male. **M.** Sensory vesicle of second article of maxillary palp of male.

tooth of claw subtriangular, its size and shape as in *wygodzinskyi.* Abdominal sterna with only delicate setae. Eighth sternite, gonapophyses, and genital fork without special characters; shape of cercus and paraproct as in figure 115J.

Male. Length of wing 4.2–4.9 mm (average 4.5). Color as in *wygodzinskyi,* but scutum almost invariably with anterior portion, sides and median longitudinal areas piceous; scutum appearing blackish when observed without magnification.

Holoptic. Shape and proportions of antennal segments as in figure 115F; ratio length/width of first flagellomere 1:0.43–0.56. Sensory vesicle of maxillary palp subglobular, small, with short but distinct neck (fig. 115M). Wing as in female, but Sc only with 22–23 hairs. Hind leg as in figure 115I. Fore basitarsus 15.0–15.5 times, hind basitarsus 5.7–6.3 times as long as wide. Calcipala considerably beyond middle of second tarsomere (fig. 115L). Genitalia as in *wygodzinskyi.*

Pupa. Cocoon slipper shaped, covering pupa to middle of anterior portion of thorax, leaving only anterior declivity of thorax, head, and gills exposed (fig. 117G, H, K). Color of cocoon light brown, tightly woven but thin, translucent when not covered by foreign particles. Length of cocoon along dorsum 4.0–4.3 mm. Total length of pupal body 4.2–5.0 mm; cephalopterothecal length 2.8–3.0 mm. Gills (figs. 116A, 117G, H, J, K) with 18 branches, both gills combined forming a forwardly facing peltate structure. General structure of gills much as in *wygodzinskyi,* but 11th branch invariably rounded apically, and 12th and 16th branches not over twice as long as 13th. Cuticular processes of gill filiform (fig. 116A, D, F), extending to apex of all branches including 12th and 16th. Shape and proportion of frontoclypeus of female and male as in figure 116B, C, with distinctly verrucose platelets distributed as in *wygodzinskyi.* Facial trichomes rather short, spinelike. Thorax with three dorsocentral trichomes in shape of spinelike setae (fig. 117I) and two dorsolateral trichomes in shape of delicate

Fig. 116. *G. brevis.* Pupa. **A.** Pupal gill flattened out. **B.** Outline of frontoclypeus, female. **C.** Same, male. **D.** Apex of 16th branch of pupal gill. **E.** Trichome of thorax of pupa, with platelets. **F.** Distal portion of seventh branch of pupal tergites. **G.** Abdominal tergites I and II.

setae (fig. 116E). Platelets distinctly verrucose, irregularly distributed (fig. 116E). Onchotaxy of I–II tergite of abdomen (fig. 116G) as in *wygodzinskyi.*

Mature larva. Length 8.0–8.5 mm; width of head capsule 0.8 mm. Body shape as usual for the genus; ventral papillae well developed. Color as in *wygodzinskyi.* Cephalic apotome ornamented as in figure 117E. Antenna reaching to or slightly beyond level of apex of cephalic fan stem, faintly pigmented. Shape of antenna as in figure 117F; ratio of segments

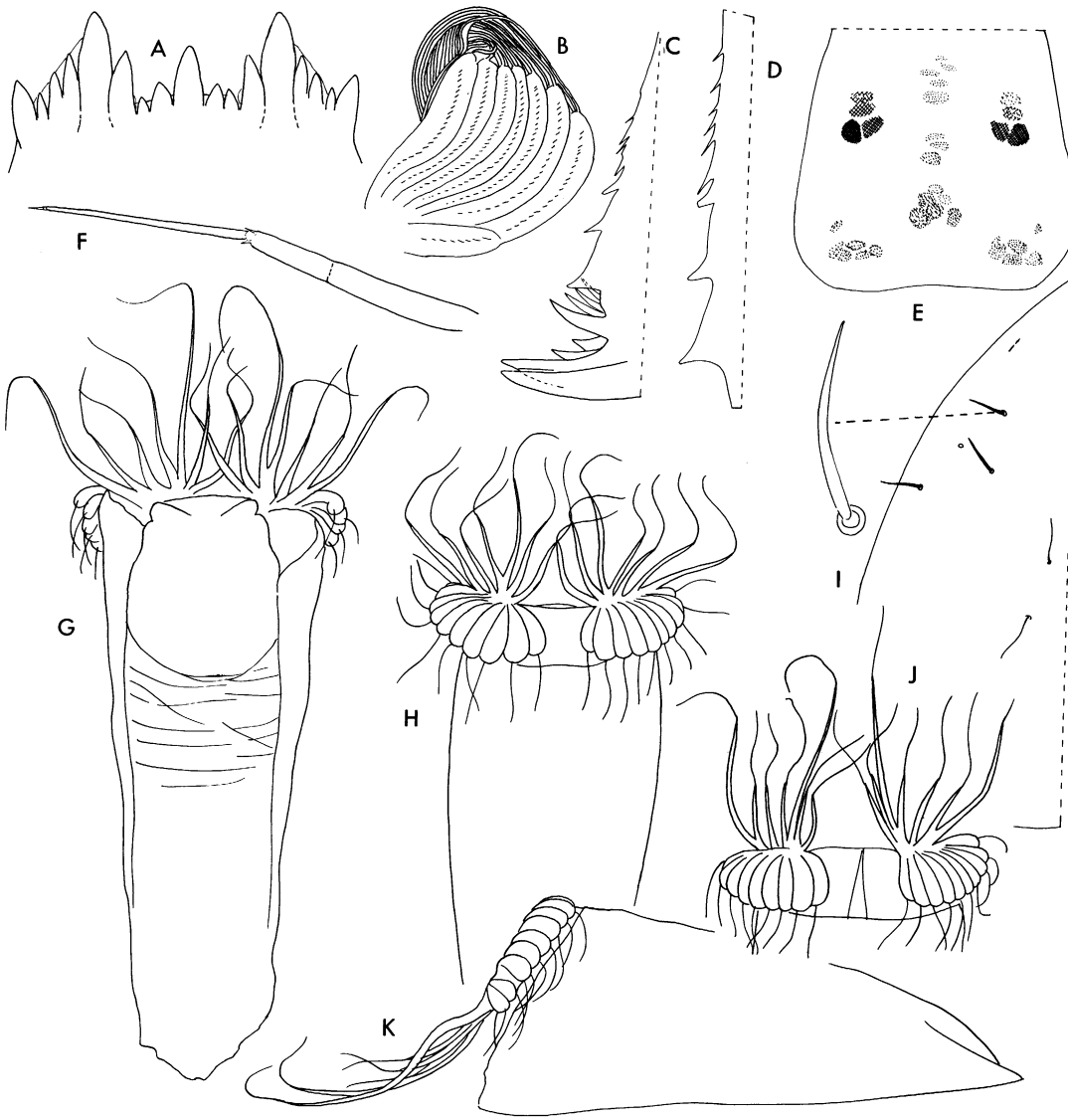

Fig. 117. *G. brevis.* A–F. Larva. **A.** Distal portion of hypostomium. **B.** Gill histoblast. **C.** Apex of mandible. **D.** Mandibular serrations. **E.** Cephalic apotome. **F.** Antenna. G–K. Pupa. **G.** Pupa with cocoon, ventral view. **H.** Pupa with cocoon, dorsal view. **I.** Portion of thorax, with trichomes. **J.** Anterior portion of pupa. **K.** Pupa with cocoon, side view.

I–III = 1:0.5:1.2–1.35. Terminal sensillum slender, 4.5–5.0 times as long as wide at base. Cephalic fan with 30–33 large rays; small teeth only slightly decreasing in size within each group. Mandible (fig. 117C, D) with 8 to 11 inner teeth and 7 to 10 marginal serrations. Maxillary palp slender, about three times as long as wide at base. Hypostomial teeth as shown in figure 117A. Apex of median tooth falling considerably short of apex of corner tooth, but reaching to or slightly beyond level of third intermediate tooth apex. Line connecting apex of median tooth to apex of fourth lateral tooth intersecting several teeth lying between them. Seven to nine marginal serrations and three to four hypostomial setae in each row. Cervical sclerites as shown for *cormonsi.* Gill histoblast as illustrated (fig.

117B). Recurrent struts locally pigmented, distally obsolescent. Perianal scales limited to 1 + 1 distinct patches at dorsal arms of X-shaped sclerite, not forming circumanal ring. Crochet ring with 80–90 rows of approximately 18 hooks each.

HOLOTYPE: COLOMBIA: *Cundinamarca:* near road from Usme to Paramo de Chisaca (or Sumapaz), 3300 m, July 27, 1967, male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female, allotype, 12 males, and 3 females, paratypes (all reared, and with their associated pupal exuviae), pupae, and larvae; ibid., July 11, 1967, pupae; ibid., 3100 m, 2 males, and 3 females, paratypes (all reared, and with their associated pupal exuviae); Paramo de Chisaca (or Sumapaz), 3500 m, June 30, 1965, one pupa; ibid., 3700 m, June 30, 1965, pupae and larvae; ibid., July 2, 1965, 2 males, 1 female, paratypes (all reared, and with their associated pupal exuviae); road from Bogota to Choachi, 3100 m, July 13, 1967, 1 female, paratype (reared, and with associated pupal exuviae); ibid., 3250 m, July 19, 1967, pupae and larvae; road from Zipaquira to Pacho, 3050 m, July 22, 1967, 1 male, paratype (reared, and with associated pupal exuviae), pupae; E of La Siberia, 3150 m, Aug. 26, 1969, 1 male, 4 females, paratypes (all reared, and with their associated pupal exuviae). *Boyaca:* Paramo de Tota, 3400 m, July 8, 1967, 1 male, paratype (reared, and with associated pupal exuviae).

All of the above specimens were collected by P. and B. Wygodzinsky and are in the collections of the AMNH.

ETYMOLOGY: From the Latin *brevis,* short, an allusion to the relatively short 12th and 16th branches of the gill of the pupa.

BIOLOGY: *G. brevis* is sympatric with its close relative, *G. wygodzinskyi,* over much of its range. The species also seem to be synoecious in many locations, because pupae of both species occur together in large numbers. The biological data given for *wygodzinskyi* also apply to the present species. It would seem, however, that their altitudinal ranges do not coincide fully, although they overlap: *G. brevis* has been collected between 3100 and 3700 m, and *wygodzinskyi* between 2400 and 3300 m. A possible hybrid between the two species is shown in figure 121.

DISCUSSION: This species is very close to *wygodzinskyi,* and can be distinguished from it with certainty only in the pupal stage; the main differential characters are given in the key.

Gigantodax wygodzinskyi
Moncada, de Hoyos and Bueno
Figures 118A–S, 119A–I, 120A–Q

Gigantodax wygodzinskyi Moncada, de Hoyos and Bueno 1981: 302–311, 34 figs.

DIAGNOSIS: Differs from *brevis,* the most closely related species by the 11th branch of pupal gill being pointed apically, 12th and 16th branches more than twice as long as wide, and with short, setalike cuticular projections restricted to base of branches.

REDESCRIPTION: *Female.* Length of wing, 3.9–4.6 mm. Color as described for *cormonsi,* but scutellum as dark as metanotum. Frontal angle 30–35°. Fronto-ocular triangle higher than wide (fig. 118C). Shape and proportions of antennal segments as in figure 118B. Mandible with ±30 teeth along only inner margin. Maxilla with 28–30 teeth. Terminal segment of maxillary palp slightly longer than penultimate (fig. 118A). Second segment of maxillary palp suboval, ratio length/width = 1:0.45–0.53. Sensory vesicle large, with distinct neck (fig. 118D). Sc with 33–38 hairs. R with setae arranged in one or two incomplete rows. R_1 with two irregular rows of setae, interspersed with numerous spinules beginning at level of insertion of Sc on C. Rs with setae arranged in three irregular rows. A_1 reaching wing margin. Shape and proportions of fore and hind leg segments as in figure 118L, H. Hind basitarsus 6.6–6.7 times as long as wide. Calcipala considerably surpassing middle of second tarsomere (fig. 118P). Basal tooth of claw as in figure 118F. Abdominal sterna only with delicate hairs. Cercus and paraproct as in figure 118G; eighth sternite with gonapophyses and genital fork without special characters.

Male. Length of wing 3.9–4.4 mm. Color as described for *cormonsi,* but posterior tergites uniformly dark except on posterior margin.

Holoptic. Shape and proportions of antennal segments as in figure 118J; ratio length/width for first flagellomere 1:0.50–0.59. Api-

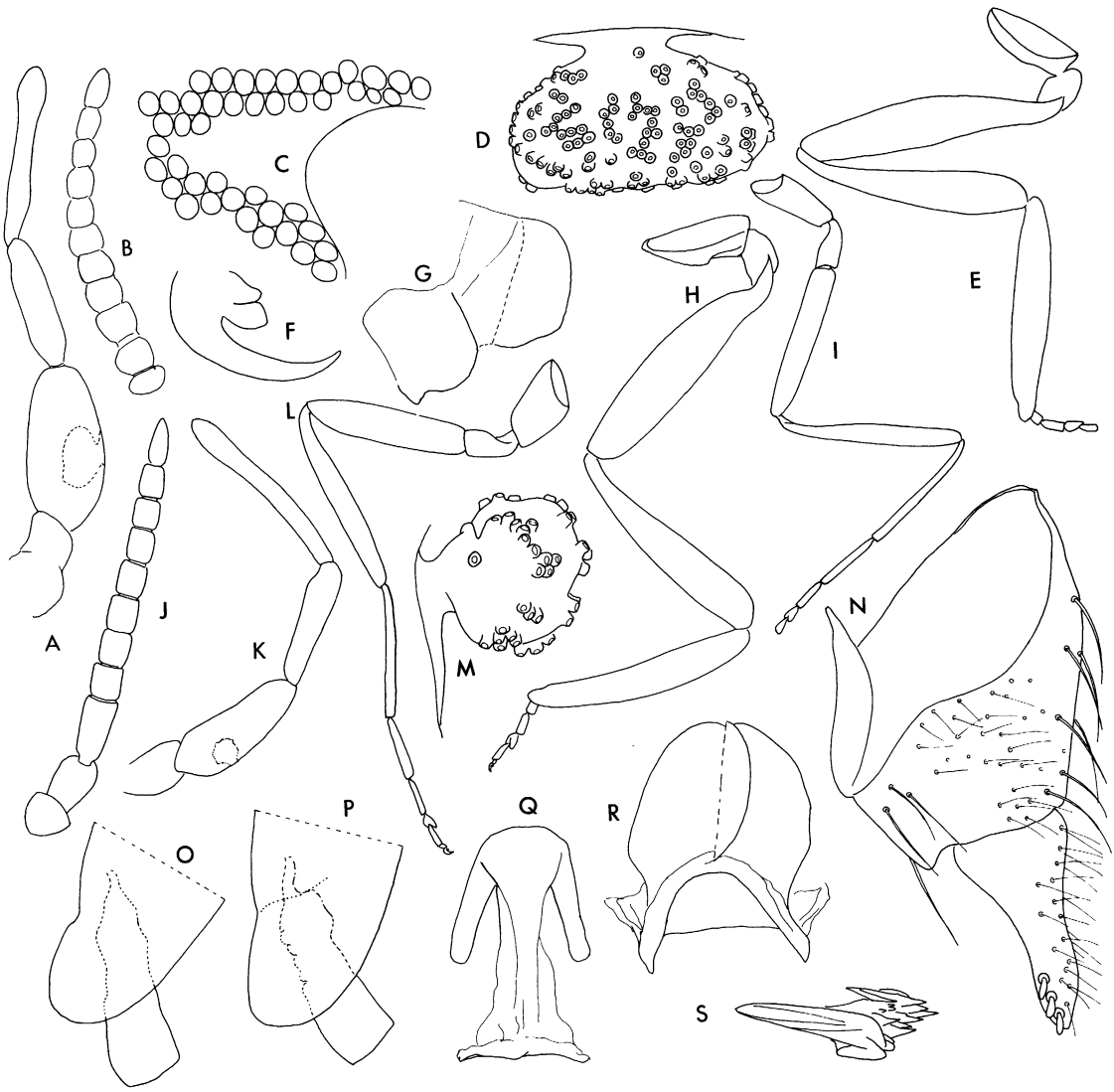

Fig. 118. *Gigantodax wygodzinskyi.* A–D. Female. **A.** Maxillary palp. **B.** Antenna. **C.** Fronto-ocular triangle. **D.** Sensory vesicle of maxillary palp. **E.** Hind leg of male. F–H. Female. **F.** Claw. **G.** Cercus and paraproct. **H.** Hind leg. I–K. Male. **I.** Foreleg. **J.** Antenna. **K.** Maxillary palp. **L.** Foreleg of female. M–O. Male. **M.** Sensory vesicle of maxillary palp. **N.** Basimere and distimere. **O.** Calcipala with second tarsal segment. **P.** Calcipala of female, with second tarsal segment. Q–S. Male. **Q.** Median sclerite. **R.** Ventral plate. **S.** Endoparameral organ.

cal segment of maxillary palp slightly longer than penultimate (fig. 118K). Sensory vesicle small, subglobular, with distinct neck (fig. 118M). Wing much as in female. Sc with 30–33 hairs; setae on R as in female. Shape and proportions of leg segments as in figure 118E, I. Fore basitarsus 15.5–15.7, hind basitarsus 5.4–5.9 times as long as wide. Calcipala extended well beyond middle of second tarsomere (fig. 118O). Distimere over two-thirds as long as basimere, with two or three apical spines (fig. 118N). Main body of ventral plate about as long as wide (fig. 118R). Median sclerite and endoparameral organ as shown in figure 118Q, S.

Pupa. Cocoon slipper shaped, covering

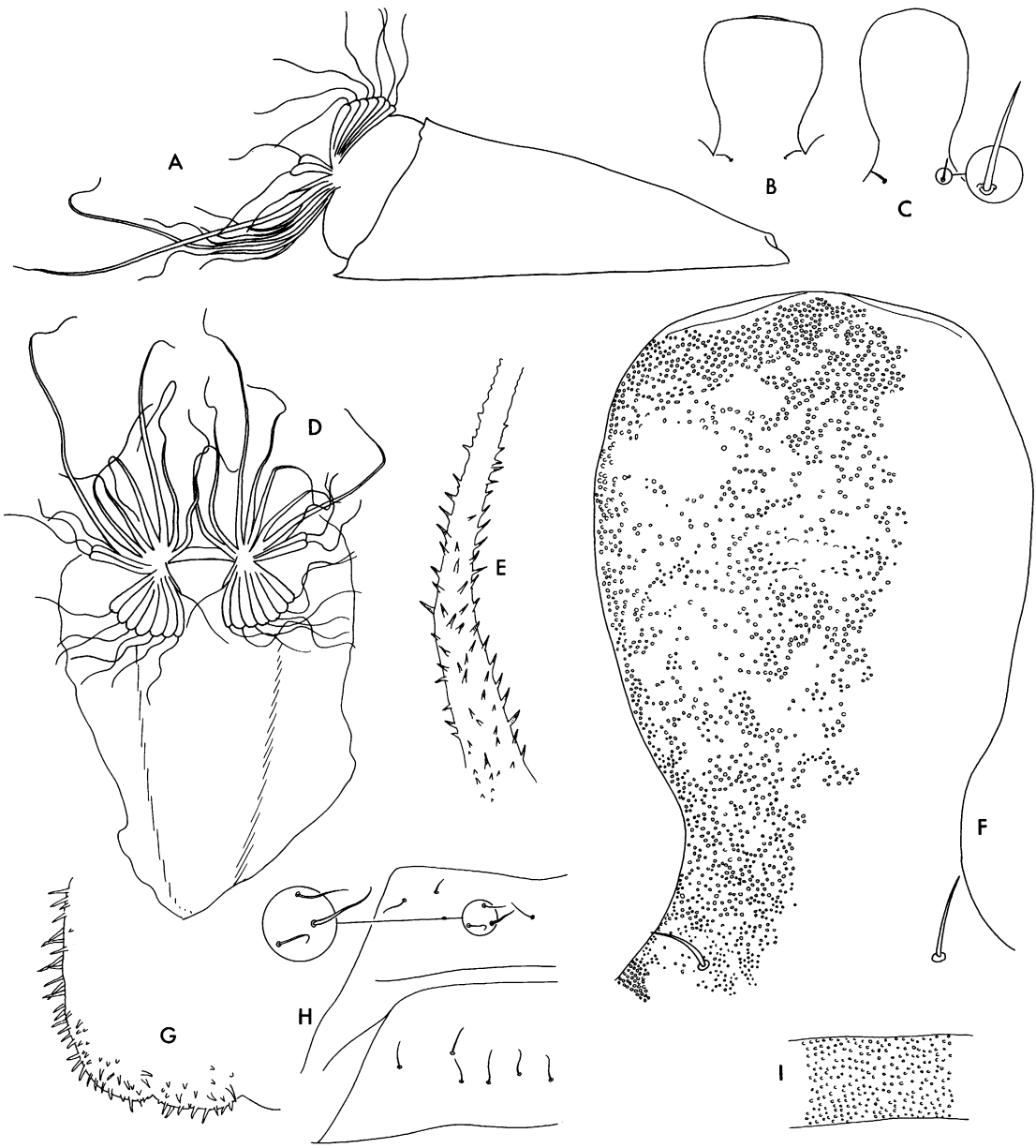

Fig. 119. *G. wygodzinskyi.* Pupa. **A.** Pupa in cocoon, lateral view. **B.** Frontoclypeus of female pupa. **C.** Same, male. **D.** Pupa in cocoon, dorsal view. **E.** Distal portion of gill branch. **F.** Frontoclypeus of male. **G.** Distal area of upper group of fused branches. **H.** Chaetotaxy of abdominal tergites I and II. **I.** Microstructure of respiratory filament.

pupa dorsally to middle of thorax, leaving anterior portion of thorax, head, and gills exposed (figs.119A, D, 120A). Color of cocoon light brown, tightly woven but somewhat translucent; length of cocoon along dorsum 4.2–4.8 mm. Total length of body of pupa 4.5–5.0 mm; cephalopterothecal length 2.7 mm. Gills with 18 branches, forming a complex structure, roughly perpendicular to longitudinal axis of pupal body (figs. 119A, D, 120A–C). First branch free, short, pointed apically. Second to eighth branches forming

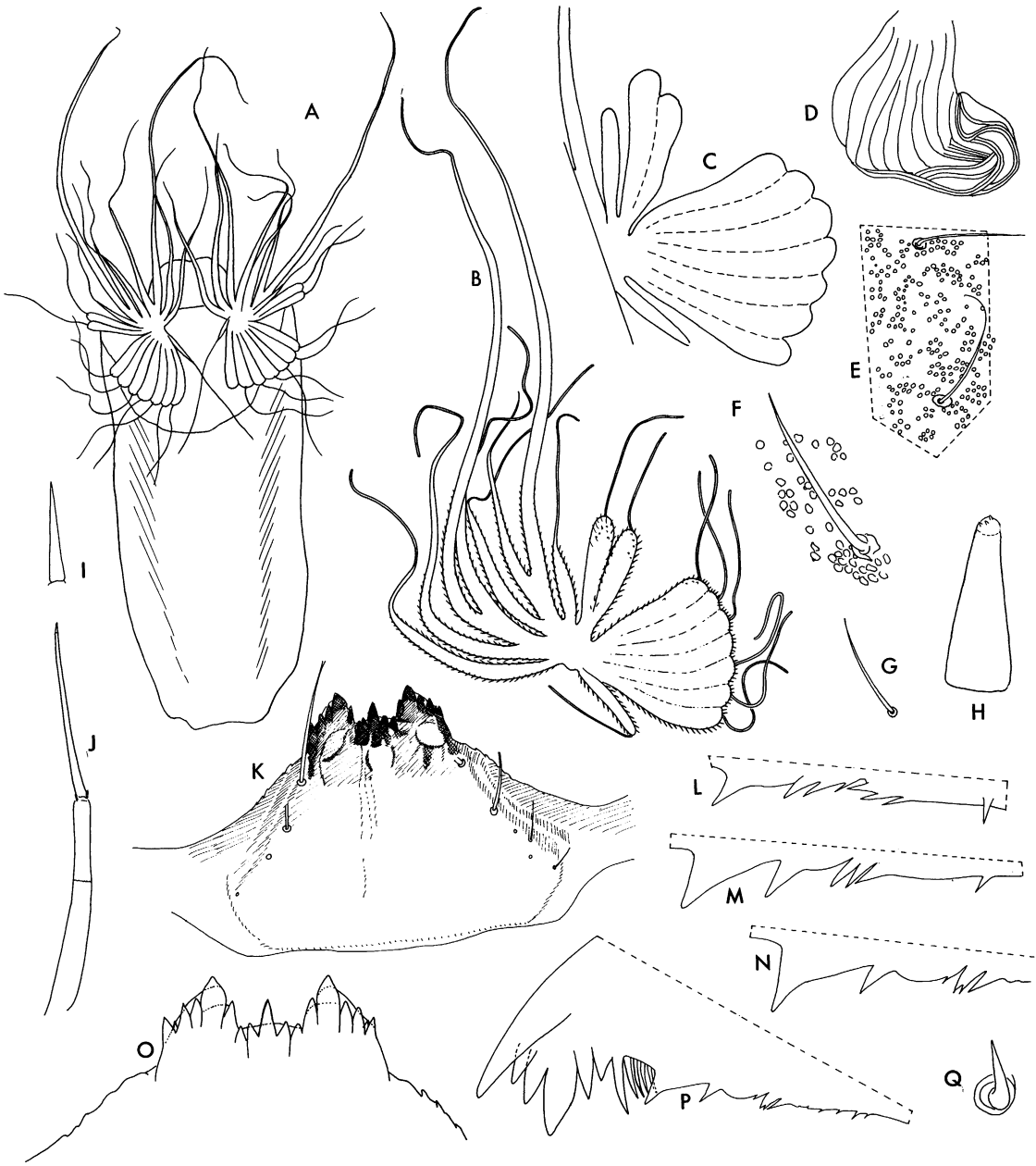

Fig. 120. *G. wygodzinskyi.* A–G. Pupa. **A.** Pupa in cocoon, dorsal view. **B.** Gill. **C.** Portion of gill. **D.** Gill histoblast. **E.** Detail of thorax, with trichomes. **F.** Dorsolateral trichome of thorax. **G.** Anterosublateral trichome of abdominal tergite III. H–P. Larva. **H.** Maxillary palp. **I.** Terminal sensillum of antenna. **J.** Antenna. **K.** Hypostomium. **L–N.** Mandibular serrations. **O.** Anterior portion of hypostomium. **P.** Distal portion of mandible. **Q.** Hook of tergite IV of pupa.

a subvertical forwardly facing shield; branches completely fused, of subequal length, apices broadly rounded, forming a continuous wavy outline. Remaining branches free for all or most of their length. Ninth and 10th branches arising from very short common trunk, shorter than second to eighth branches, rounded apically. Eleventh branch single,

shorter than the two preceding, generally rounded but in some cases pointed apically. Twelfth and 13th branches arising from common trunk; 13th about as long as branches forming dorsal shield, but gradually narrowing toward pointed apex; 12th over three times as long as 13th, very gradually narrowing to filiform apex. Fourteenth, 17th, and 18th branches free, similar to 13th although somewhat longer, especially 17th. Fifteenth and 16th branches arising from common trunk; 15th similar to 12th. Areas of contact of branches forming dorsal shield indicated by rows of small perforations (fig. 120B, C). Apices of all branches with long respiratory filaments. Surface of much of gills covered with spinelike cuticular processes (fig. 119E, G) extending to apex of shorter branches (1st to 11th) but falling short of apical portion of 12th to 18th branches. Microstructure of gill filaments as in figure 119I. Shape and proportions of frontoclypeus of female and male as in figure 119B, C, with faintly verrucose platelets most closely spaced along anterior and lateral margins, more sparse on disc (fig. 119F). Facial trichomes in shape of slender spinelike setae. Thorax with three dorsocentrals in shape of slender spinelike setae (fig. 120F), and two dorsolaterals in shape of delicate hairs (fig. 120E). Platelets of thorax faintly verrucose, arranged in irregular pattern. Abdominal tergite I with a few small hairs (length 30–50 μm, and 1 + 1 larger, very strong, spinelike setae, lengths 80–105 μm). Setae of tergite II slightly stouter than hairs of I, but not spinelike, their length 40–60 μm (fig. 119H). Tergites III and IV each with 4 + 4 short but narrowly pointed hooks (fig. 120Q). Anterosublateral setae (fig. 120G) hairlike. Setae of tergites V–VIII very slender, their length on tergite VII 80–90 μm. Spinecombs on tergites VI–VIII, continuous, consisting on tergite VII of 28–33 spines, their length 20–30 μm, viz., one-fourth to one-third length of setae of this tergite. Specialized setae of eighth and ninth segments from straight to variously curved and branched. Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 8.0–8.5 mm; width of head capsule 0.8–0.83 mm. Body shape as usual for genus; ventral papillae well developed. Ground body color of larva whitish, with diffuse overall dark pigment, most noticeable on swollen posterior portion of abdomen. Head light yellow, with markings distinct. Hypostomial bridge faintly darkened and with 1 + 1 sublateral spots near base. Antenna reaching apex of cephalic fan stem, faintly pigmented throughout. Shape of antenna as in figure 120J; ratio of segments I–III = 1:0.38–0.55:1.17–1.35. Terminal sensillum slender, 5–6 times as long as wide at base (fig. 120I). Cephalic fan with 23–25 large rays; small teeth subequal in size. Mandible with 10–11 inner teeth and 7–8 marginal serrations (fig. 120L–N). Maxillary palp slender, about three times as long as wide at base (fig. 120H). Hypostomium with apex of median tooth falling considerably short of apex of corner tooth but reaching to or slightly surpassing level of third intermediate teeth apices (fig. 120K). Line connecting apex of median tooth to apex of first lateral tooth intersecting several teeth lying in between. Hypostomium with 8–10 lateral serrations, and 3–4 hypostomial setae in each row. Cervical sclerites as shown for *cormonsi.* Histoblast as in figure 120D. Perianal scales limited to 1 + 1 distinct patches at dorsal arms of X-shaped sclerite, not forming circumanal ring. Anal armature generally with recurrent struts not well pigmented distally. Crochet ring with approximately 100 rows of 16–18 hooks each. Rectal gills not examined.

MATERIAL EXAMINED: COLOMBIA: *Cundinamarca:* near road from Usme to Paramo de Chisaca (or Sumapaz), 3300 m, July 27, 1967 (P. and B. Wygodzinsky; AMNH), 21 males, 13 females (all reared, and with their associated pupal exuviae) pupae, larvae; ibid., July 11, 1967 (P. and B. Wygodzinsky; AMNH), 1 pupa; ibid., 3100 m, July 27, 1967 (P. and B. Wygodzinsky; AMNH), 2 males, 10 females (all reared, and with their associated pupal exuviae) pupae, larvae; stream 5 km S of Usme, 3000 m, July 27, 1969 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal exuviae) pupae, larvae; road from Bogota to Choachi, 3000–3050 m, July 13, 1967 (P. and B. Wygodzinsky; AMNH), 1 pupa; 2 km SE of Alban, 2400 m, August 6, 1967 (P. and B. Wygodzinsky; AMNH), pupae; ibid., Aug. 24, 1969 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal

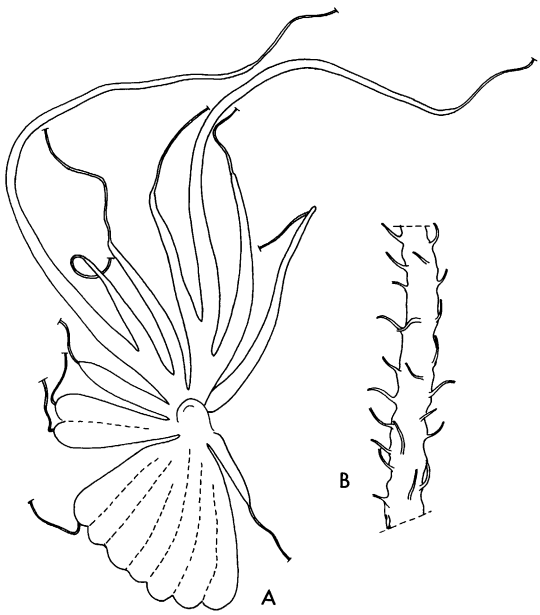

Fig. 121. Possible hybrid between *G. brevis* and *G. wygodzinskyi*. **A.** Pupal gill. **B.** Surface structure of narrow portion of gill branch.

exuviae); Buenos Aires, near La Siberia, E of La Calera, 3050 m, July 17, 1967 (P. and B. Wygodzinsky; AMNH), 1 pupa; ibid., Aug. 26, 1969 (P. and B. Wygodzinsky; AMNH), 16 males, 23 females (reared, and with their associated pupal exuviae), pupae, and larvae; ibid., 3150 m, Aug. 26, 1969 (P. and B. Wygodzinsky; AMNH), 3 males, 2 females, reared, and with their pupal exuviae.

BIOLOGY: The aquatic instars of this species were found on the undersides of watercress leaves and on grasses, roots, and other vegetation trailing in small streams and irrigation ditches in pastures and other open land; in a few instances, pupae were collected from the undersides of stones resting on the bottom of the watercourses. The width of the watercourses did not surpass 30 cm, and their depth 5 cm. The temperature varied between 12 and 17°C. There was considerable organic material deposited on the bottom of the streams and on the vegetation where *G. wygodzinskyi* was collected, but the water itself was clear.

DISCUSSION: The pupal gills of this and the following species, although quite different from those of all other species of the genus known to us, indicate a possible relationship to the *cormonsi* group. The dorsal shield is formed by the fusion of branches 2–8, and is obviously homologous to the shield formed by the fusion of branches 1–8 in *cormonsi* and its allies. Although branches 9–18 are free in *wygodzinskyi* and the following species, *brevis*, branches 12 and 16 are strikingly longer than any of the others in both groups. The adults of *wygodzinskyi* and *brevis* are more difficult to differentiate from those of the *cormonsi* group; the narrow frons of the females (frontal angle 30 to 35°, as opposed to 50°) is the most striking difference.

We did not see the type material, but the description and illustrations, especially of the gill branches, are so peculiar that we think our material corresponds to this species. Also, we saw pupae in the AMNH that were sent by Paulina de Hoyos; they are similar to our specimens. The material studied by us was collected in the same area.

Gigantodax wygodzinskyi × *brevis*

Figure 121A, B

DISCUSSION: Among hundreds of pupae of *G. wygodzinskyi* and *G. brevis* collected near the road from Usme to Paramo de Chisaca at 3300 m, on July 27, 1967, we have found two specimens which in some characters are intermediate between the two species mentioned. The two pupae share with *wygodzinskyi* the pointed 11th gill branch and the very elongate 12th and 16th branches, and with *brevis* the fact that the cuticular processes extend on all arms up to the point of insertion of the respiratory filament (fig. 121A, B). The cuticular processes themselves (fig. 121B) are intermediate between the long, hairlike ones of *brevis*, and the short, spinelike ones of *wygodzinskyi*.

We hypothesize that these specimens represent hybrids between *wygodzinskyi* and *brevis*. These two species are closely related and sympatric, synoecious, and synchronous in at least part of their range where the postulated hybrids were collected. Although most pupae of this group are easily identified as belonging to either *brevis* or *wygodzinskyi*, the hypothesis of an occasional breakdown of the mechanisms of reproductive isolation is not improbable and seems to be confirmed

by the finding of specimens morphologically intermediate between the two possible parent species.

Gigantodax leonorum, new species
Figure 122A–K

DIAGNOSIS: Differs from *abalosi,* the most closely related species, by its larger size larvae and adult, and the perianal scales which do not form a ring.

DESCRIPTION: *Female.* Very similar to female of *abalosi,* but larger; wing length 4.5–5.0 mm. Second segment of maxillary palp rather elongate, ratio length/width = 1:0.4 (fig. 122F).

Male. Very similar to male of *G. abalosi,* but wing length 4.1–4.2 mm. Hind tarsus 5.9–6.0 times as long as wide.

Pupa. Much as in *abalosi.* Cocoon comparatively large, in many cases covering part of thorax of pupa. Length of cocoon along dorsum, 4.0 mm. Length of body of pupa 4.2–4.5 mm; cephalopterothecal length 2.5–2.9 mm. Gills (fig. 122A, B) as in *abalosi.* Facial trichomes spinelike (fig. 122J, K). Thorax with platelets on dorsal portion (fig. 122C, E), forming irregular clusters, in some cases arranged in rosettes. All platelets verrucose. Thoracic trichomes consisting of two or three dorsocentrals, and one or two delicate hairlike dorsomedials. Chaetotaxy of abdomen as in *G. cormonsi*; anterosublateral setae of tergites IV and V very slender (fig. 122H); hooks of abdominal IV as in figure 122I; a few of the specialized setae of eighth and ninth segments branched or grapnel shaped.

Mature larva. Length 9.5 mm; width of head capsule 0.85–0.9 mm. General shape and color as in *abalosi.* Head pattern distinct. Antenna longer than stem of cephalic fan, very faintly pigmented. Ratios of antennal segments I–III = 1:0.4–0.5:1.2–1.4; terminal sensillum slender, 5.0–5.5 times as long as wide at base. Cephalic fan as in *abalosi.* Mandible with 9–10 inner teeth and five or six marginal serrations (fig. 122G). Maxillary palp, hypostomium, and cervical sclerites as in *abalosi.* Perianal scales inconspicuous, few in number, restricted to region of arms of X-shaped sclerite, not forming a ring. Recurrent struts not well developed. Crochet ring with 90–95 rows, composed of 15–17 hooks each. Rectal gills not examined.

HOLOTYPE: ECUADOR: *Pichincha:* Quito-Papallacta road, 3300 m, July 20–Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female allotype, 12 males, 8 females, paratypes (all reared, and with their pupal skins, pupae, and larvae. ECUADOR: *Pichincha:* along Santo Domingo de los Colorados road, 2650 m, Aug. 19, 1969 (P. and B. Wygodzinsky; AMNH), 1 male (reared, with its pupal exuviae), 1 pupa. *Cotopaxi:* NW slope of Mount Cotopaxi, 3500 m, July 26–Aug. 5, 1969 (P. and B. Wygodzinsky; AMNH), pupae.

ETYMOLOGY: This species is named for Dr. Luis A. Leon and his family, who helped so much, in so many ways, when the first author and his wife carried out fieldwork in Ecuador.

BIOLOGY: Larvae and pupae of G. *leonorum* were collected in slightly shaded irrigation ditches and small streams up to 30 cm wide and 10 cm deep, with water temperatures from 9.5 to 10°C. The water was clear, although organic material was deposited on the stream bottom and occasionally on the leaves where the specimens were found. Larvae and pupae were collected in large numbers on trailing grasses and on the undersides of watercress leaves, and pupae at least in one irrigation ditch were on the undersurfaces of large stones resting on the bottom of the watercourse.

DISCUSSION: Superficially, this species is very similar to *G. abalosi* with which it agrees in the structure of the highly modified pupal gills. The imagos of *leonorum* are larger than those of *abalosi*; the facial and thoracic trichomes of *leonorum* are spine shaped instead of hairlike, as in *abalosi.* The larva of *leonorum* is somewhat larger than that of *abalosi,* but the mandible of the former has fewer marginal teeth (5–6 versus 6–10); furthermore, in *Leonorum* the perianal scales are much less numerous than in *abalosi,* and do not form a ring.

The Ecuadorian specimens examined come from several localities within a range of about 100 km. In most specimens, the platelets on the thorax of the pupa are clustered in irregular groups (fig. 122C), as in *abalosi.* In specimens collected at the road from Aloag to

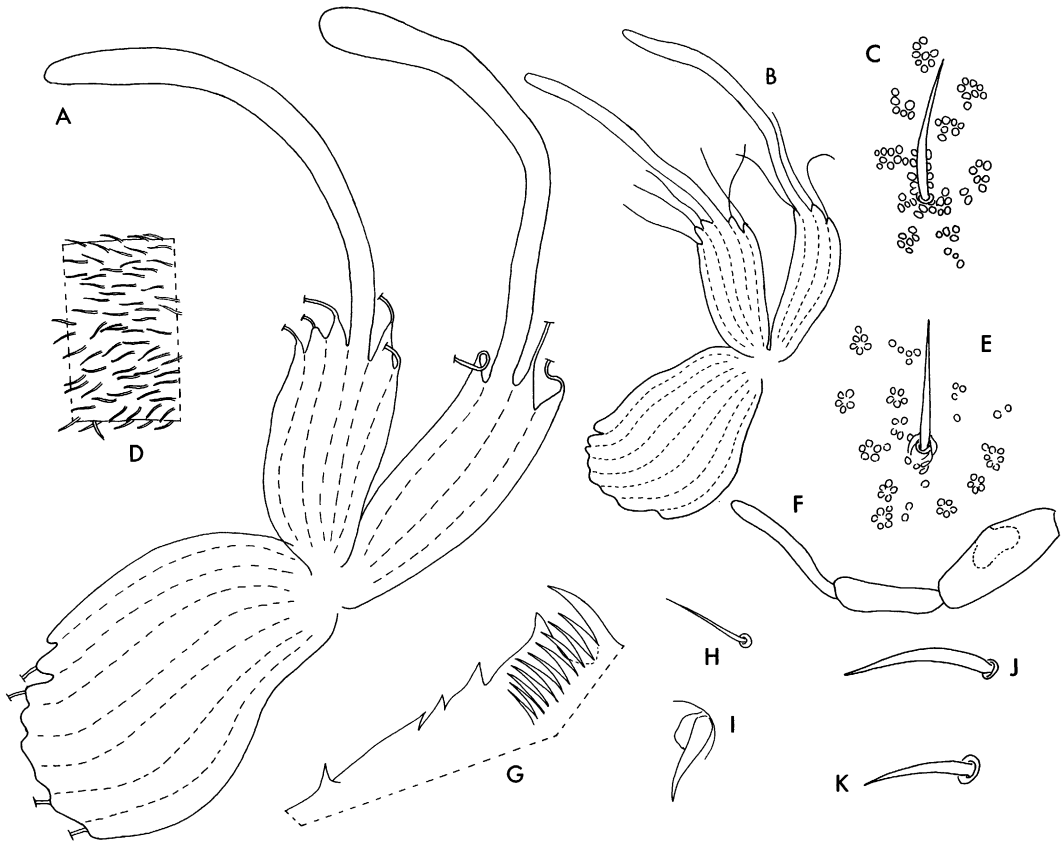

Fig. 122. *Gigantodax leonorum.* **A, B.** Gills of pupa. **C.** Platelets and trichomes of thorax of pupa. **D.** Microstructure of elongate gill branches. **E.** Platelets and trichomes of thorax of pupa. **F.** Maxillary palp of female. **G.** Apical portion of mandible of larva. **H.** Anterosublateral trichome of abdominal tergite III. **I.** Hook of tergite IV. **J, K.** Facial trichome of pupa.

Santo Domingo de los Colorados, at 2650 m, many of these platelets are arranged in a distinctly rosettelike pattern (fig. 122E), similar to that found in *G. cormonsi.*

Gigantodax sp. near *leonorum*

MATERIAL EXAMINED: COLOMBIA: *Cauca:* stream near road from Popayan to Paramo de Purace, 2500 m, Aug. 17, 1967 (P. and B. Wygodzinsky; AMNH), 1 larva; E of Silvia, 2900 m, Aug. 24, 1967 (P. and B. Wygodzinsky; AMNH), larvae.

DISCUSSION: These larvae agree with those of *leonorum,* the geographically closest species of the *cormonsi* group. Two larvae contained pharate pupae in which the cuticular processes of the free branches of their gills were setalike, as in *leonorum.* We could not examine the facial or thoracic trichomes which are decisive for identifying species in this complex, and therefore list the Colombian material as doubtfully belonging to *leonorum.*

DISTRIBUTION: Specimens of this northernmost population of the *cormonsi* complex, were found only on the west slope of the central range of the Andes in Colombia.

Gigantodax abalosi Wygodzinsky
Figures 123A–N, 124A–K, 125A–K

Gigantodax abalosi Wygodzinsky, 1958: 143–147, figs. 109–141. Vulcano, 1967: 2; 1977: 290.

DIAGNOSIS: *G. abalosi* differs from the closely related *leonorum* by the long and hairlike facial trichomes and notal trichomes of the pupa.

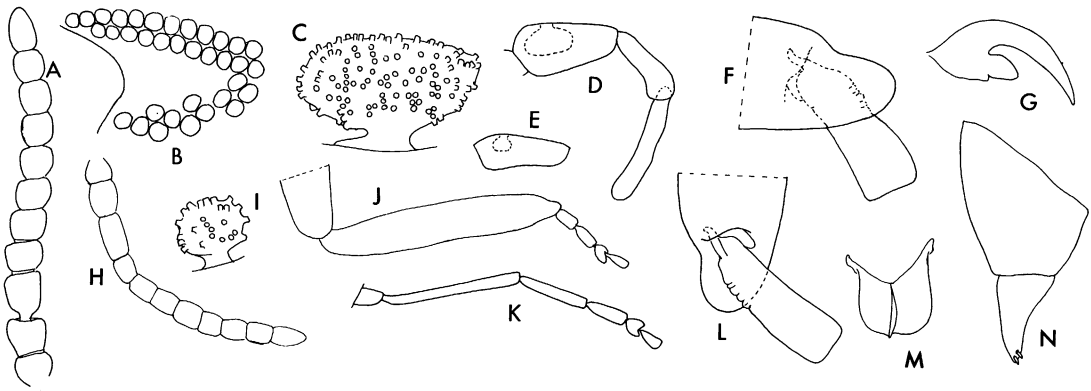

Fig. 123. *Gigantodax abalosi.* **A.** Antenna of female. **B.** Fronto-ocular triangle. **C.** Sensory vesicle of maxillary palp, female. **D.** Maxillary palp, female. **E.** Third segment of maxillary palp with sensory vesicle, male. **F.** Calcipala with second tarsal segment, female. **G.** Female claw. **H.** Antenna, male. **I.** Sensory vesicle of maxillary palp, male. **J.** Posterior tarsus, male. **K.** First pair of legs, male. **L.** Calcipala of male, with second tarsal segment. **M.** Ventral plate. **N.** Basimere and distimere.

REDESCRIPTION: *Female.* Length of wing 3.7–4.1 mm. Color as in *cormonsi* but scutum darker brown. Frontal angle 50°. Fronto-ocular triangle (fig. 123B) higher than wide. Shape and proportion of antennal segments as in figure 123A; mandible and maxilla as in *cormonsi.* Second segment of maxillary palp suboval, ratio length to width 1:0.5. Distal segment of maxillary palp less than twice as long as penultimate (fig. 123D). Sensory vesicle large, with distinct neck (fig. 123C). Chaetotaxy of wing as in *cormonsi.* Hind basitarsus 7.8 times as long as wide. Calcipala slightly surpassing level of middle of second tarsomere (fig. 123F). Claws as in figure 123G. Abdomen and genitalia as in *cormonsi.*

Male. Length of wing 3.8–4.2 mm. Color as described for *cormonsi.* Holoptic. Shape and proportions of antennal segments as in figure 123H; ratio length/width of first flagellomere, 1:0.6. Sensory vesicle (fig. 123I) small, subglobular, with distinct neck. Chaetotaxy of wing as in male of *cormonsi.* Shape and proportion of some leg segments as in figure 123J, K. Calcipala a little shorter than the middle of second tarsomere. Ratio length/width of fore basitarsus 14.0, of hind basitarsus, 6.2–6.3. Genitalia very close to those of *cormonsi.* Basimere, distimere, and ventral plate as in figure 123M, N.

Pupa. Cocoon leaving free most of thorax as in figure 124A, B; length along dorsum 3 mm. Total length of pupal body 4.2–4.5 mm; cephalopterothecal length 2.2–2.4 mm. General structure of gills as in *cormonsi*; 12th and 16th branches frequently, although not invariably, thickened distally and broadly rounded at apex (fig. 124A–E). Cuticular processes elongate, bristlelike (fig. 124F). Shape and proportions of frontoclypeus of female and male as in figure 124J, K, with numerous very distinct platelets. Facial trichomes slender, hairlike. Thorax with platelets on dorsal surface forming clusters but not arranged in rosettes. Platelets slightly verrucose. Thoracic trichomes with two or three long, slender, hairlike dorsocentrals (fig. 124G). Chaetotaxy of abdomen much as in *cormonsi,* but setae of first abdominal tergite (30–40 μm) and of second abdominal tergite (70–75 μm) much longer (fig. 124I). Setae of distal segment as in figure 124H.

Mature larva. Length 7.2–8.0 mm; width of head capsule 0.7–0.8 mm. Body shape as in figure 125A, B; ventral papillae well developed. Color of larva yellowish white. Head light yellow; spots of cephalic apotome distinct but not dark. Hypostomial bridge lacking pigment. Antenna longer than stem of cephalic fan, hyaline, without perceptible pigment. Shape of antenna as in figure 125K; ratio of length of segments I–III = 1:0.45–0.48:1.06–1.09. Terminal sensillum elongate, 5.5 times as long as wide at base (fig. 125D). Cephalic fans with 30–34 large rays; each group of small teeth with units decreas-

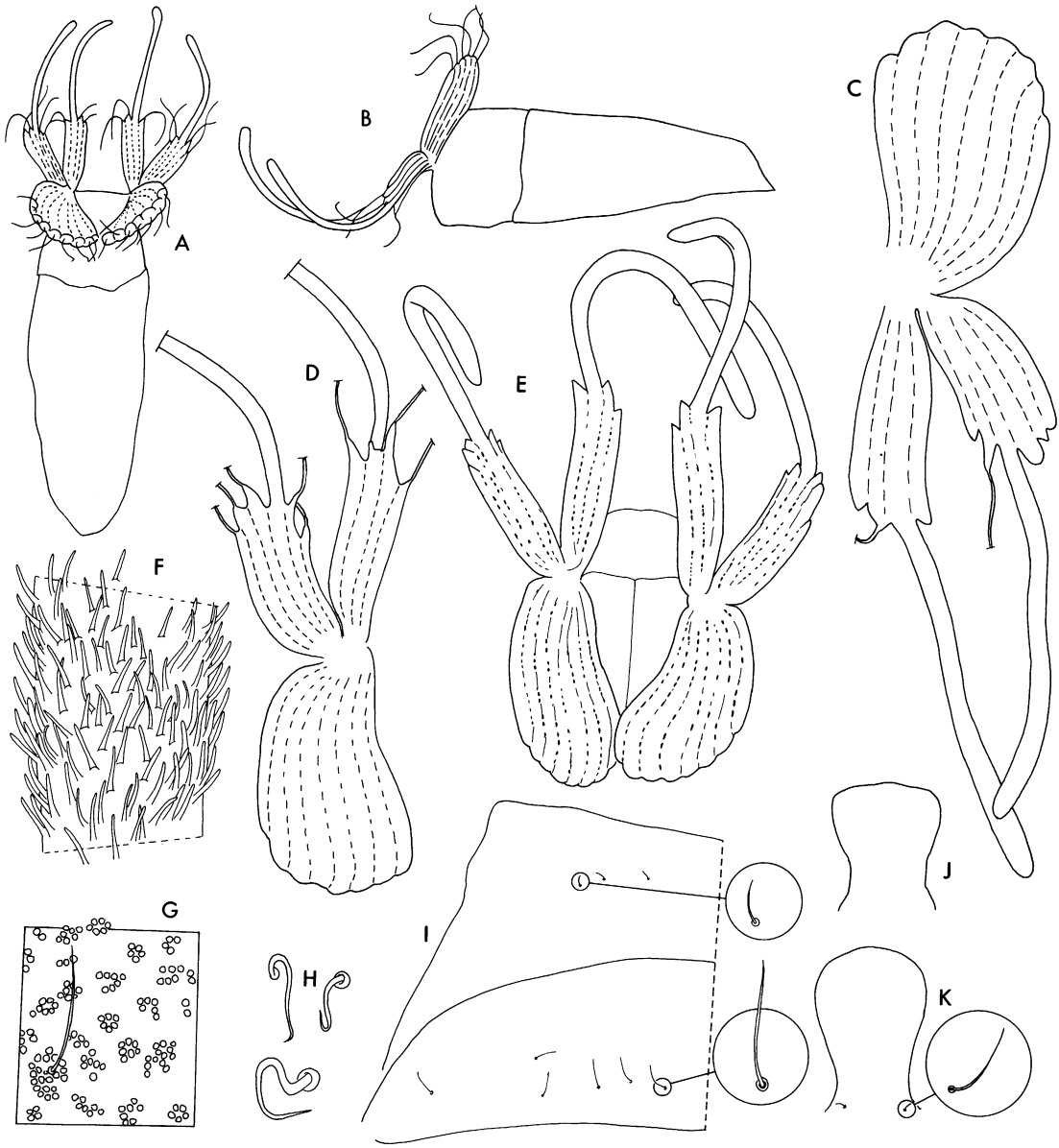

Fig. 124. *G. abalosi.* Pupa. A, B. Pupa in cocoon. **A.** Dorsal view. **B.** Lateral view. **C–E.** Gills, anterodorsal view. **F.** Cuticular processes of 12th and 16th branches. **G.** Thoracic platelets. **H.** Setae of distal segment of abdomen of pupa. **I.** Chaetotaxy of abdominal tergites I–II. **J.** Frontoclypeus of female. **K.** Same, male.

ing in size from first to last (fig. 125I). Mandibles with eight to nine inner teeth and six to ten marginal serrations (fig. 125F, G). Maxillary palp slender, slightly less than three times as long as wide at base. Hypostomial teeth (fig. 125H) much as in *G. cormonsi*; six to seven lateral serrations; two to four hypostomial setae in each row. Cervical sclerites as in *cormonsi.* Histoblast as in figure 125J, very similar to that of *cormonsi.* Perianal scales well developed, although less heavily pigmented than in *cormonsi,* numer-

ous, forming complete ring. Recurrent struts few, developed. Crochet ring with approximately 80 rows of 16–18 hooks each.

MATERIAL EXAMINED: PERU: *Lima:* Canta, valley of Chillan River, 3200 m, Oct. 28, 1972 (F. Blancas and P. Wygodzinsky; AMNH), 1 female (reared and with associated exuviae), pupae; Chacahuaro, Quebrada de Unturu, valley of Rimac River, 2600 m, Sept. 24, 1963 (A. Herrer and P. Wygodzinsky; AMNH), larvae; Surco, valley of Rimac River, 2100 m, Aug. 17, 1965 (F. Blancas and P. and B. Wygodzinsky; AMNH), pupae, larvae; between Songo and Verrugas Canyon, valley of Rimac, 2000 m, Sept. 28, 1983 (S. Coscarón; MLP), pupa.

BIOLOGY AND DISTRIBUTION: *Gigantodax abalosi* has only been found on the west slope of the Peruvian Andes at medium elevations (2100–3200 m). The aquatic stages were collected exclusively on the undersurfaces of large stones, in clear streams or irrigation ditches, at a water temperature of 15°C.

DISCUSSION: *G. abalosi* differs from *G. cormonsi* and *G. praealtus* by the setalike cuticular processes of the free branches of the pupal gills, a character *abalosi* shares with the Ecuadorian *leonorum*. The larva of *abalosi* differs from that of the other species (larvae of *praealtus* unknown) by its comparatively short third antennal segment (see description and key).

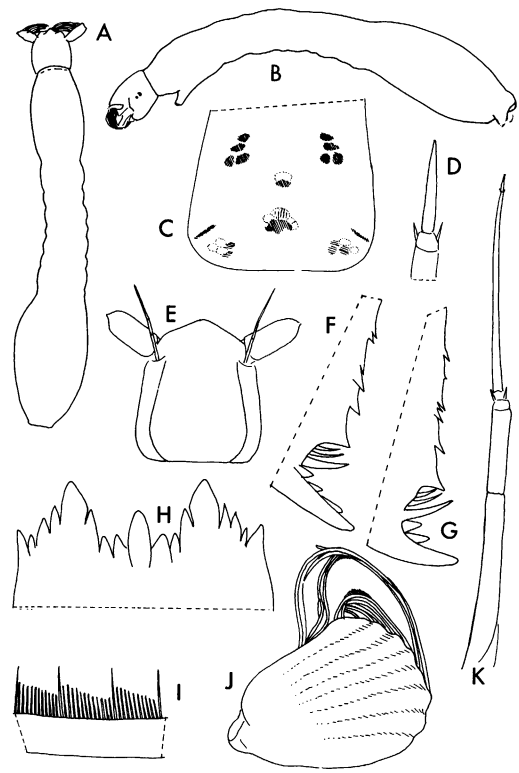

Fig. 125. *G. abalosi.* **A.** Larva, dorsal view. **B.** Larva, side view. **C.** Cephalic apotome, with color pattern. **D.** Terminal sensillum of antenna. **E.** Head, dorsal view, highly schematic. **F, G.** Apex of mandibles. **H.** Hypostomial teeth. **I.** Teeth of ray of cephalic fan. **J.** Gill histoblast. **K.** Antenna.

Gigantodax cormonsi, new species
Figures 126A–V, 127A–J, 128A–R

DIAGNOSIS: Imagos reddish brown, scutum with central area darker, and calcipala reaching to level of second tarsomere, pupal gill with 18 branches fused into three shieldlike groups, with individual components of dorsal shield projecting slightly beyond margin of shield, antenna of larva distinctly projecting beyond level of apices of stem of cephalic fan, and gill histoblast without cuticular processus on branches.

DESCRIPTION: *Female.* Length of wing 4.3–4.7 mm. Head blackish; pilosity brass colored. Antenna and maxillary palp dark brown; scapus and pedicellus from lighter brown to orange. Scutum light reddish brown, central portion darker. Scutellum yellowish brown, metanotum darker brown. Pleural region light reddish brown, with faint purple pollinosity. Thoracic setae brass colored. Wing translucent, veins light yellowish brown. Setae on stem vein dark, the remaining setae light colored. Halter yellowish white. Legs pale yellow, bases and apices of femora and tibiae darkened; setae concolorous. Abdominal terga piceous with hind margin whitish, narrowly so on anterior, more extensively so on posterior segments. Abdominal hairs brass colored.

Frontal angle approximately 50°. Frontoocular triangle slightly higher than wide (fig. 126D). Shape and proportions of antennal segments as in figure 126C. Mandible with 22–25 teeth (fig. 126B). Maxilla with approximately 23 teeth. Second segment of maxillary palp suboval, ratio length/width 1: 0.56–0.58. Apical segment of maxillary palp

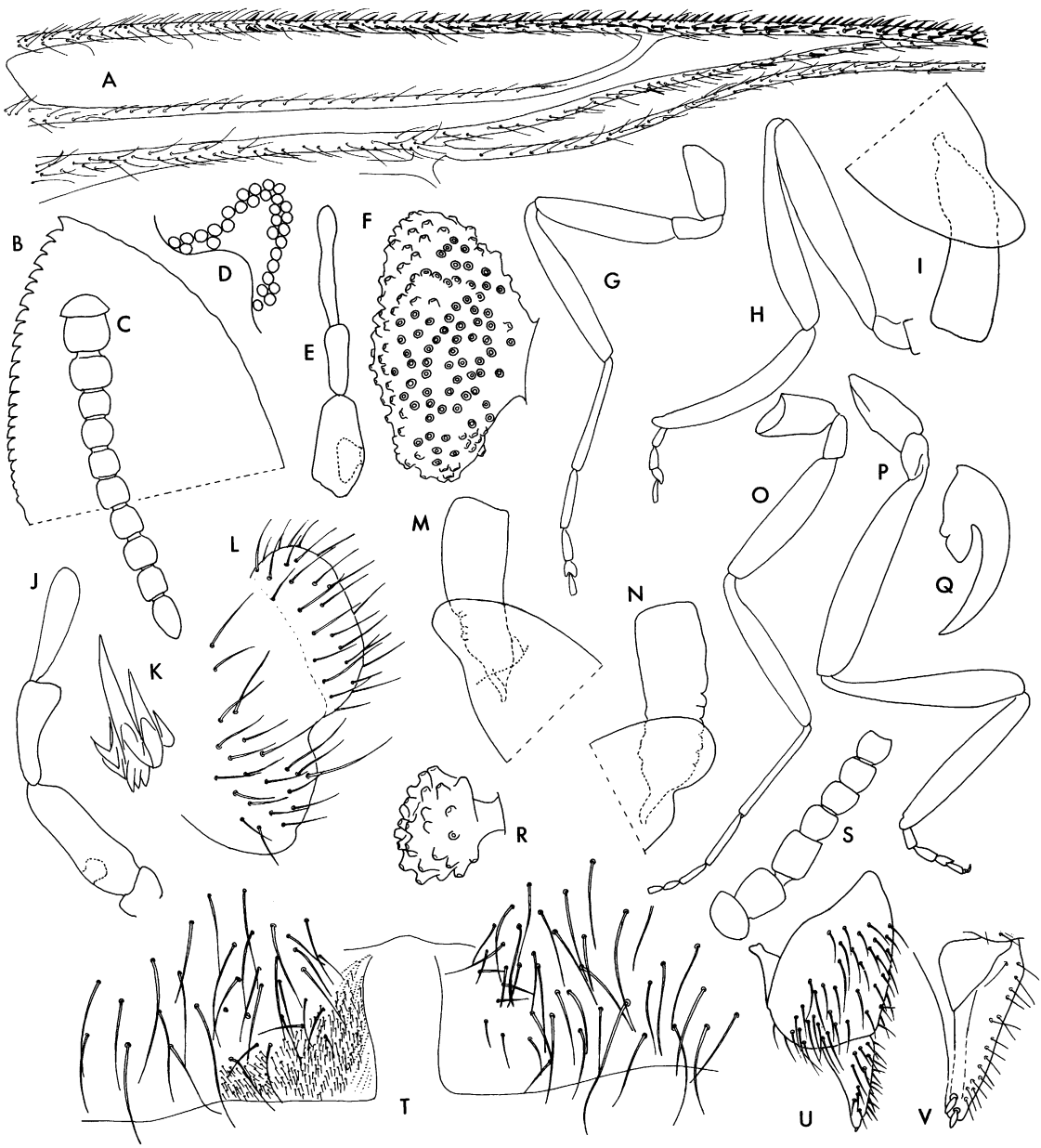

Fig. 126. *Gigantodax cormonsi.* A–I. Female. **A.** Portion of wing. **B.** Apex of mandible. **C.** Antenna. **D.** Fronto-ocular triangle. **E.** Maxillary palp. **F.** Sensory vesicle of maxillary palp. **G.** Foreleg. **H.** Hind leg. **I.** Calcipala. **J.** Maxillary palp of female. **K.** Endoparameral organ. **L.** Cercus and paraproct. M–P. Male. **M.** Calcipala. **N.** Same, different specimen. **O.** Foreleg. **P.** Posterior leg. **Q.** Claw of female. **R.** Sensory vesicle of maxillary palp of male. **S.** Basal articles of antenna of male. **T.** Portion of sternite VIII of female, with gonapophyses; microtrichia shown only on left side. **U.** Basimere and distimere, under surface. **V.** Same, upper surface.

less than twice as long as penultimate (fig. 126E). Sensory vesicle large, with very short neck (fig. 126E). Sc with about 30 hairs. R with setae arranged in two or three rows. R_1 with setae in one or two rows; spinules present, well developed, beginning at level of insertion of Sc on C, interspersed among hairs in one or two rows. R_s with setae arranged in

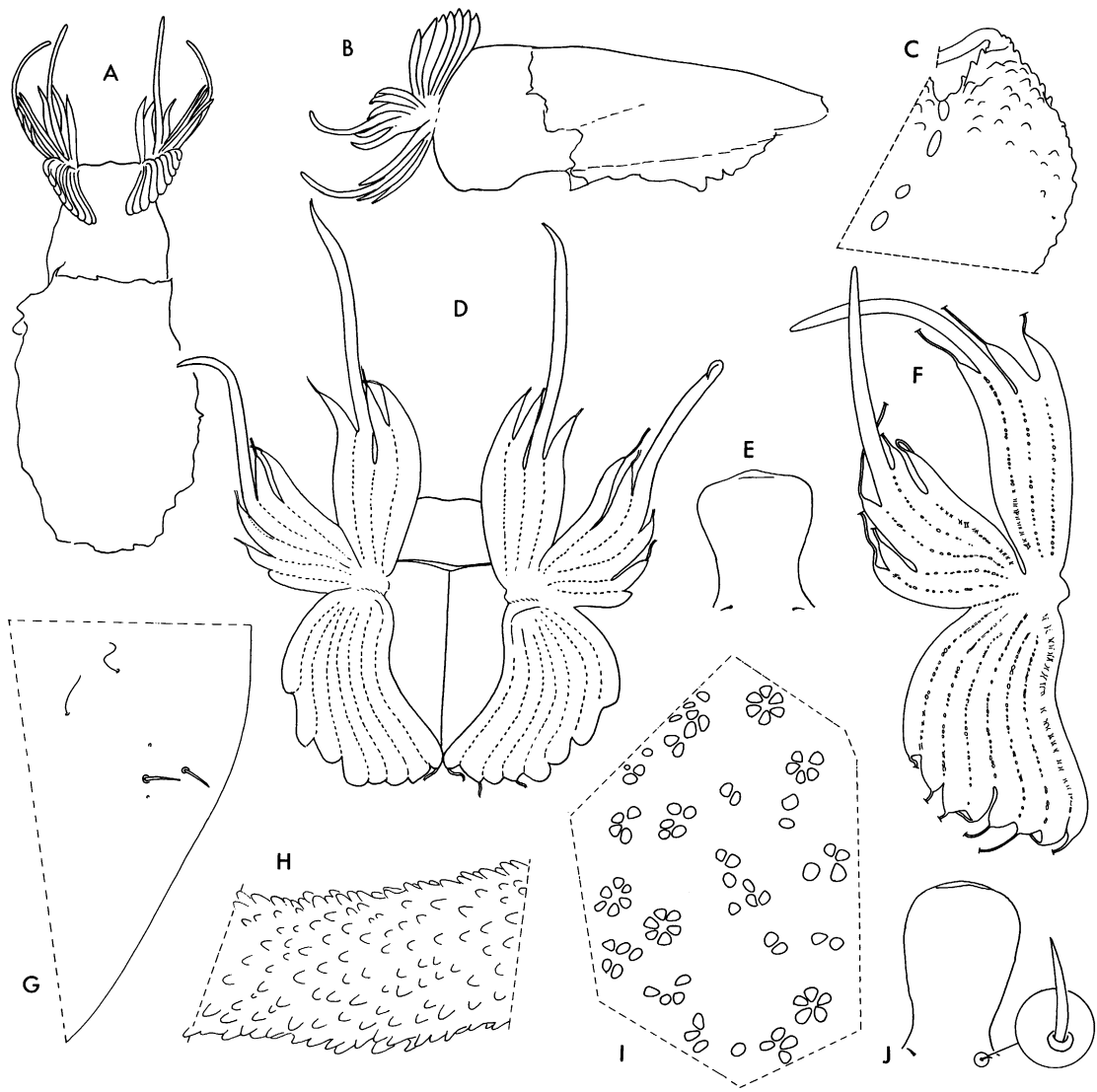

Fig. 127. *G. cormonsi.* Pupa. **A.** Pupa in cocoon, dorsal view. **B.** Same, side view. **C.** Apex of gill branch, with extreme base of respiratory filament. **D.** Head and gills, front view. **E.** Outline of frontoclypeus, female. **F.** Gill. **G.** Portion of thorax, with trichomes. **H.** Surface structure of sixteenth gill branch. **I.** Platelets of thorax. **J.** Outline of frontoclypeus of male.

two irregular rows (fig. 126A). A_1 almost reaching wing margin. Shape and proportions of fore and hind leg segments as in figure 126G, H. Calcipala reaching middle of second tarsomere (fig. 126I). Hind basitarsus from 6.9 to 7.6 times as long as wide. Basal tooth of claw large, subtriangular (fig. 126Q). Abdominal sterna with delicate hairs. Cercus, paraproct, and gonapophyses as in figure 126L, T.

Male. Length of wings 4.1–4.3 mm. Color as in female, but reddish color of scutum more saturated. Holoptic. Shape and proportions of antennal segments as in figure 126S; ratio length/width of first flagellomere 1:0.74–0.83. Last segment of maxillary palp approximately as long as penultimate (fig. 126J). Sensory vesicle (fig. 126R) small, subglobular, with distinct neck. Chaetotaxy of wing as in female, but Sc with only 17–20 hairs. Shape and proportions of fore and hind leg segments as in figure 126O, P. Fore basitarsus 12.0–

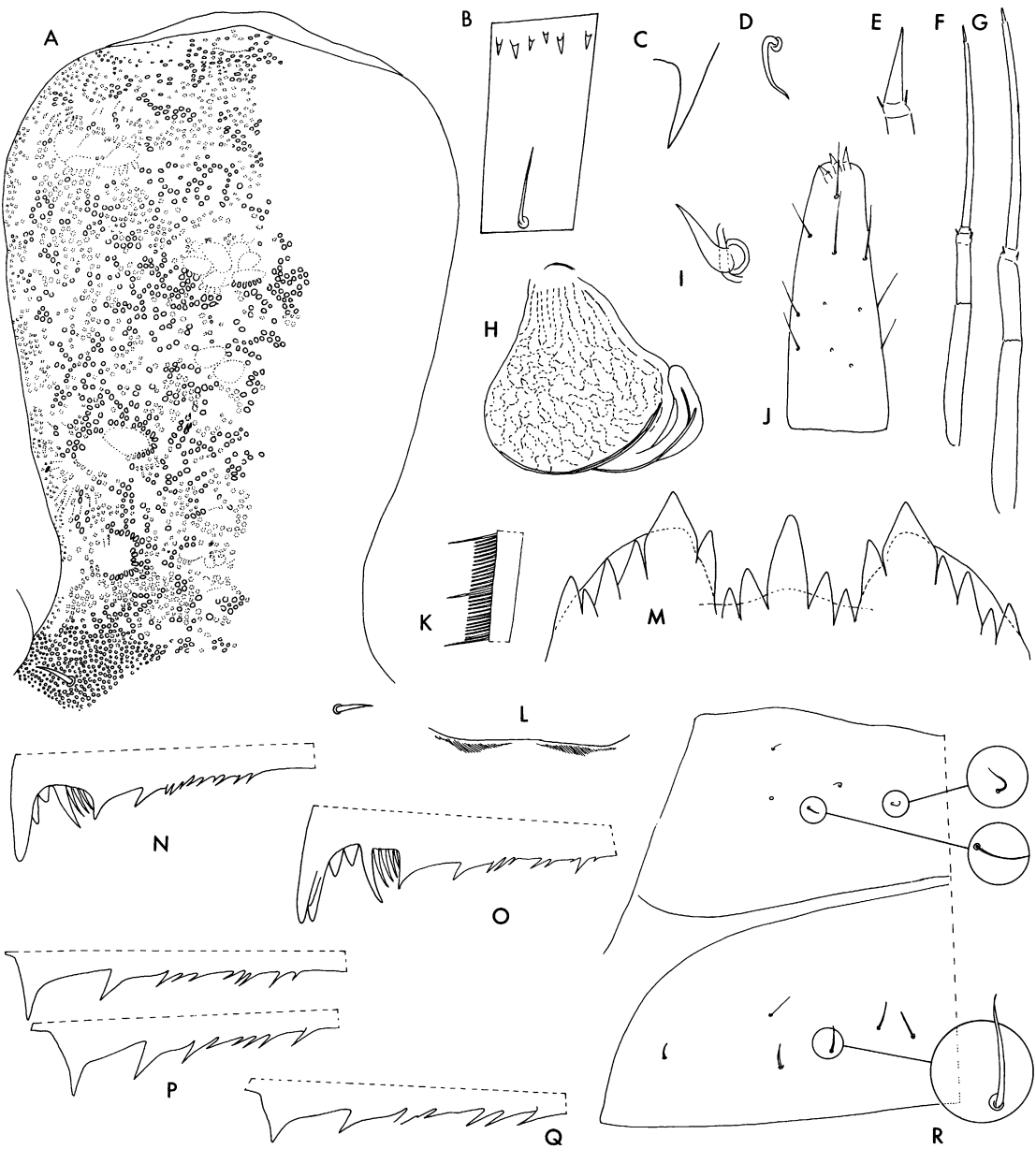

Fig. 128. *G. cormonsi.* A–D. Pupa. **A.** Frontoclypeus of male pupa. **B.** Portion of tergite VII. **C.** Terminal spine of abdomen. **D.** Seta of tergite VIII. **E.** Terminal sensillum of antenna. **F, G.** Antenna. **H.** Gill histoblast. **I.** Hook and seta of tergite III. **J.** Maxillary palp. **K.** Teeth of rays of cephalic fan. **L.** Cervical sclerites. **M.** Teeth of distal portion of hypostomium. **N, O.** Apex of mandible. **P, Q.** Mandibular serrations. **R.** Chaetotaxy of abdominal tergites I and II.

15.0 times that of hind basitarsus, 6.65–7.0 times as long as wide. Calcipala reaching to middle of second tarsomere (fig. 126M). Distimere over two-thirds as long as basimere, with two apical spines (fig. 126U, V). Main body of ventral plate as long as wide. Endoparameral organ as in figure 126K.

Pupa. Cocoon small, covering pupa only

to base of abdomen; thorax, head, and gills free (fig. 127A, B). Color of cocoon very light brown, whitish in natural habitat, tightly woven but translucent; length of cocoon along dorsum approximately 3.0 mm. Total length of body of pupa up to 5.0 mm; cephalopterothecal length 2.3–2.7 mm. Gill with 18 branches fused into three shieldlike structures perpendicular to longitudinal axis of pupal body (fig. 127D, F). Dorsal shield formed by fusion of 1st to 8th branches, lateral shield by fusion of 9th to 14th, and ventral shield by fusion of 15th to 18th. Areas of contact of branches indicated by line of small perforations. Apices of components of dorsal shield rounded or angular apically, projecting little, if any, beyond margin of shield. Lateral and ventral shields with apices of individual components pointed, distinctly projecting beyond margin of shields; 12th and 16th branches elongate, projecting beyond margin of shield by length of same, from narrowly rounded to pointed apically. Apices of all branches (except 12th and 16th) with respiratory filaments (rarely intact in preserved material). Apices of short and free portions of long branches with short cuticular tubercles (fig. 127C, H). Shape and proportions of frontoclypeus of female and male as in figure 127E, J; with numerous platelets, some very distinct, some with faint outlines (fig. 128A).

Facial trichomes short, spinelike. Thorax with platelets on dorsal portion arranged in rosettelike pattern (fig. 127I). All platelets smooth. Dorsocentral trichomes consisting of two short, pointed spines, dorsolaterals of two very delicate hairs (fig. 127G). Setae of abdominal tergite I very short (15–20 μm) and delicate; setae of tergite II much larger (30 μm) and more spinelike (fig. 128R). Tergites III and IV each with 4 + 4 short hooks (fig. 128I); anterosublateral setae strong, hairlike. Setae of tergites V–VIII slender, length on tergite VII 85–100 μm. Spine-combs on tergites VI–VIII continuous, consisting on tergite VII of 30–35 spines, length 15–20 μm, viz., one-fifth the length of setae of this tergite (fig. 128B). Specialized setae of eighth and ninth segments irregularly shaped but not branched, grapnellike (fig. 128D). Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous. Terminal spines of abdomen as in figure 128C.

Mature larva. Length 8–10 mm; width of head capsule 0.8–0.97 mm. Body shape as commonly seen in the genus; ventral papillae well developed. Color of larva from yellowish white to white. Head light yellow. Spots of cephalic apotome faint. Hypostomial bridge lacking pattern elements. Antenna distinctly longer than stem of cephalic fan, hyaline, pigment not perceptible. Shape of antenna as in figure 128F, G; ratio of segments I–III = 1: 0.41–0.47:1.30–1.39. Terminal sensillum somewhat elongate, ratio length/width = 4.1 (fig. 128E). Cephalic fan with 31–35 large rays, their teeth as in figure 128K, the small teeth subequal in size. Mandible (fig. 128N–Q) with 8–11 inner teeth and 6–10 marginal serrations. Maxillary palp slender, about three times as long as wide at base (fig. 128J). Hypostomium (fig. 128M) with apex of median tooth falling short of apex of corner tooth but distinctly beyond level of third intermediate tooth apex. Line connecting apex of median tooth to apex of fourth lateral tooth intersecting several teeth lying in between. Hypostomium with seven to nine lateral serrations. Three to four hypostomial setae in each row. Cervical sclerites as shown in figure 128L. Histoblast in figure 128H, basically with irregular striations; cuticular processes obsolescent and only on free portions of long branches. Perianal scales well developed, extremely numerous, forming complete ring. Recurrent struts not well developed. Crochet ring with 82–85 rows composed of 18–20 hooks each.

HOLOTYPE: PERU: *Junin:* Tarma, Chacabamba, on Palcomayo-San Pedro de Cajas-Junin road, 3700 m, July 15, 1965 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female, allotype, 3 males, 11 females, paratypes (all reared, and with their associated pupal exuviae). PERU: *Junin:* Huarihuaran, 3 km SW Huyaricolca, 3900 m, July 12, 1965 (P. and B. Wygodzinsky; AMNH), 1 pupa, larvae. *Cuzco:* Juampar, 3450 m, April 19, 1971 (S. Coscarón; MLP), pupae.

ETYMOLOGY: This species is named for Mr. Matthew Cormons, who first pointed out its distinctiveness.

BIOLOGY: This is a high-altitude species which breeds in small, clear streams. The temperature of the streams at the locality near Tarma was between 10 and 11°C. Larvae and pupae were found near the shore of the streams, mostly on the undersurfaces of leaves of watercress, and generally only one individual per leaf. Larvae and pupae were also encountered on the surface of a large rock covered by a thin sheet of falling water.

DISCUSSION: Similar species are *praealtus, leonorum,* and *abalosi.* The differences with *praealtus* are indicated in the discussion for that species. *Gigantodax leonorum* and *abalosi* have similar but different gill morphology, and the tegumentary process is more slender and elongate.

Gigantodax praealtus, new species
Figure 129A–Q

DIAGNOSIS: Differs from *cormonsi,* the most closely related species, by the pupal gill branches projecting much beyond margin of shield, with their apical portions elongate, pointed, and the thoracic platelets arranged in a distinct pattern.

DESCRIPTION: *Pharate female.* Color and wing length unknown. Frontal angle 50°. Antenna as in *cormonsi.* Maxillary palp (fig. 129A, B) with second segment rather elongate, gradually increased toward apical portion; ratio length/width = 1.43 with last segment less than twice as long as penultimate. Sensory vesicle medium-size, with short but distinct neck; mandible not examined. Shape and proportions of leg segments as in figure 129G, H. Hind basitarsus 9–10 times as long as wide. Calcipala not quite attaining middle of second tarsomere (fig. 129I). Claws as shown in figure 129L. Genital fork, spermatheca, cercus, and paraproct as in figure 129D, M, P.

Male. Unknown.

Pupa. Cocoon small, covering pupa only to base of abdomen, leaving thorax, head, and gills free. Color of cocoon light brown; tightly woven but with individual strands perceptible; translucent. Length of cocoon along dorsum about 3.0 mm. Total length of body of pupa 4.7 mm; cephalopterothecal length 2.8 mm. General structure of gills as in *cormonsi,* each gill with 18 branches. Apices of components of dorsal shield projecting beyond margin of shield by a distance equal to 2.5–3.0 times the width of free portions. Lateral and ventral shields with 12th and 16th branches much longer than the remaining, their total length unknown (fig. 129C, E). Remaining branches composing lateral and ventral shields projecting beyond margin of shields by a distance equal to length of shields. Tubercles of gill (fig. 129F) much as in *cormonsi.* Facial trichomes not examined. Setae of thorax (fig. 129N) much as in *cormonsi.* Platelets faint, especially on thorax, smooth, and not forming circles on dorsal portion of thorax. Chaetotaxy of abdomen much as in *cormonsi*; with hooks of tergite IV and sublateral setae as in figures 129K and 129O, respectively.

Larva. Unknown.

HOLOTYPE: CHILE: *Tarapaca:* 30 km E of Alto Chapa, 4100 m, April 25, 1969 (L. E. Pena; AMNH), pharate female with associated pupal exuviae.

PARATYPE: Same data as holotype, female with associated pupal exuvium.

ETYMOLOGY: From the Latin *praealtus,* very high, in reference to the high altitude at which this species occurs.

DISCUSSION: *Gigantodax praealtus* is closely related to *G. cormonsi* and *G. abalosi* with which it shares the general structure of the pupal gills. *G. praealtus* can be distinguished from both species by the strongly projecting individual components of the pupal gills, the faint platelets of the pupal thorax, and in the female, by the comparatively shorter sensory organ of the maxillary palp and the longer second tarsomere of the hind legs. *G. praealtus* is more similar to *G. cormonsi* than to *G. abalosi* regarding the cuticular processes of the branches of the pupal gill.

Gigantodax vulcanius, new species
Figures 130A–T, 131A–J, 132A–H, 178D

DIAGNOSIS: A species differing from all others by a pupal gill with a dorsal shield composed of the fusion of 1st to 14th branches and the ventral shield with a fusion of 15th to 18th branches.

DESCRIPTION: *Female.* Length of wing 4.8–5.1 mm. Head black, pilosity silver or brass colored. Antenna and maxillary palpi black;

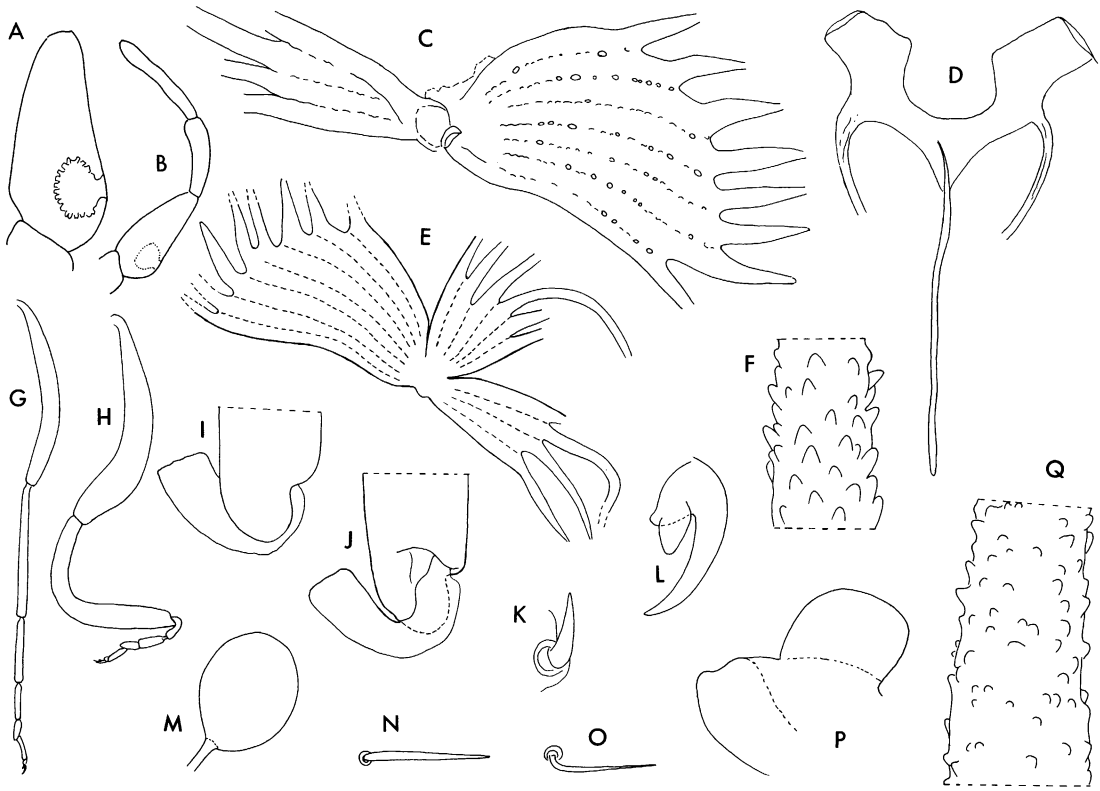

Fig. 129. *Gigantodax praealtus.* Female. **A.** Second article of maxillary palp. **B.** Maxillary palp. **C.** Gill, with one group of branches missing. **D.** Genital fork. **E.** Gill. **F.** Surface structure of gill branch. **G.** Foreleg. **H.** Hind leg. **I, J.** Calcipala, with second tarsal article. **K.** Hook of tergite IV. **L.** Claw. **M.** Spermatheca. **N.** Dorsal trichome of thorax of pupa. **O.** Anterosublateral trichome of tergite III. **P.** Cercus and paraproct. **Q.** Detail of gill branch.

scapus, pedicellus, and base of first flagellomere, reddish orange. Scutum reddish brown, of varied intensity, centrally somewhat darker, in many specimens with narrow whitish median longitudinal line. Scutellum and metanotum colored as *nasutus.* Pleural region light reddish brown, with faint purple pilosity. Thoracic setae brass colored. Wing translucent; veins yellow. Area between Sc and R distinctly yellowish; apical portion of Sc near insertion on C conspicuously pigmented with brown. Setae of stem vein dark, the remaining setae light colored. Halter yellowish. Legs pale yellow, basal and apical areas of femora and tibiae with faint pigment. Abdominal terga piceous with hind margin whitish, posterior tergites with light-colored areas extending onto disc. Hairs of abdomen brass colored.

Frontal angle about 50°. Fronto-ocular triangle higher than wide (fig. 130B). Shape and proportions of antennal segments as shown in figure 130A. Mandibles with teeth only on inner margin, their number 27–29. Maxilla with approximately 25 teeth. Terminal segment of maxillary palp only slightly longer than penultimate (fig. 130G). Second segment of maxillary palp elongate, narrowed on apical half. Sensory vesicle big without distinct neck (fig. 130K). Sc with 25–27 hairs. R with setae arranged in two irregular rows. R_1 with setae in two irregular rows, interspersed with well-developed spinules beginning at, or slightly basal to, level of insertion of Sc on wing margin. R_s with setae in two irregular rows. A_1 almost attaining wing margin. Shape and proportions of fore and hind leg segments as shown in figure 130C, H. Hind

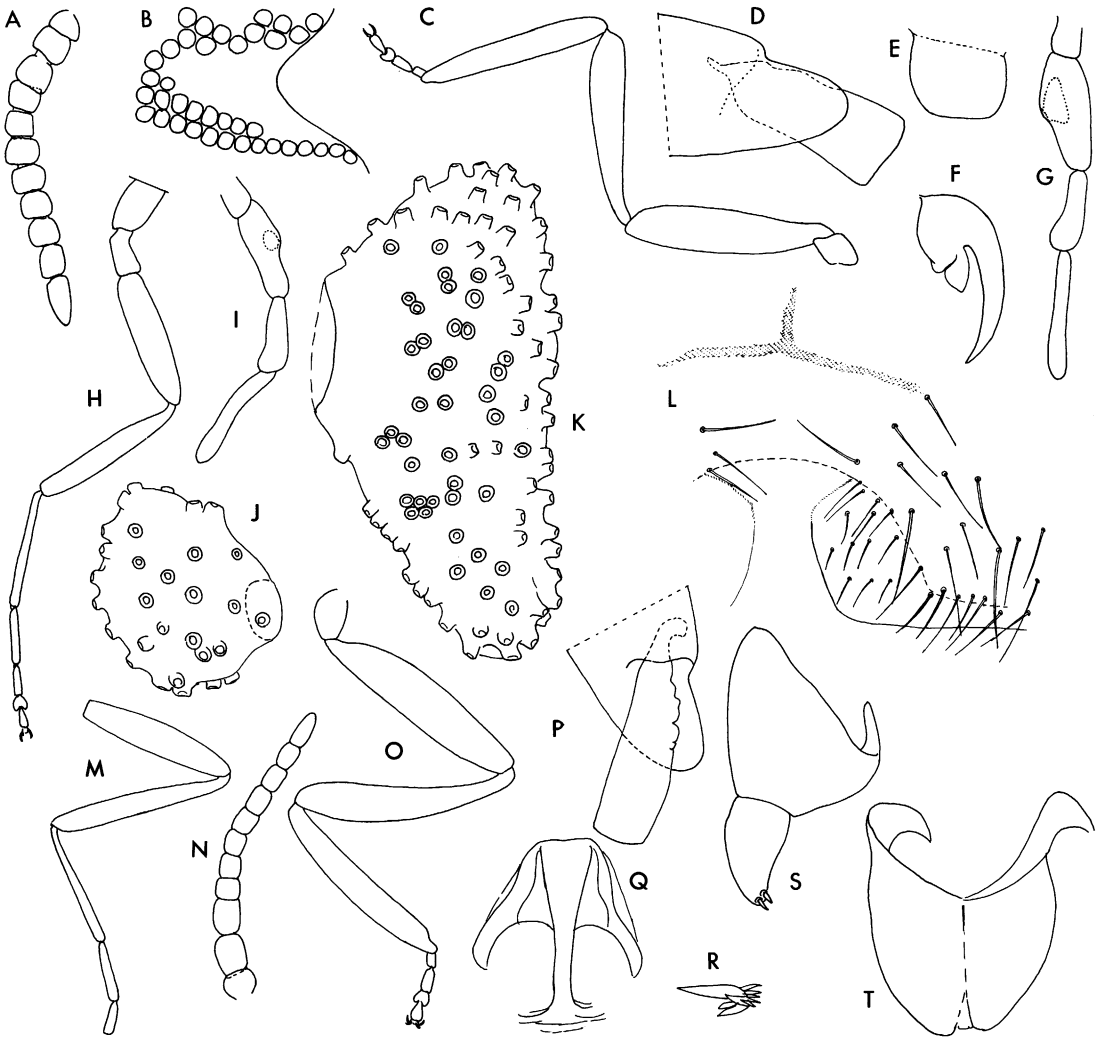

Fig. 130. *Gigantodax vulcanius.* A–H. Female. **A.** Antenna. **B.** Fronto-ocular triangle. **C.** Hind leg. **D.** Calcipala and second tarsal segment. **E.** Paraproct. **F.** Claw. **G.** Maxillary palp. **H.** Foreleg. **I.** Maxillary palp of male. **J.** Sensory vesicle of maxillary palp, male. **K.** Same, female. **L.** Portion of sternite VIII with gonapophyses. M–T. Male. **M.** Foreleg. **N.** Antenna. **O.** Hind leg. **P.** Calcipala with second tarsal segment. **Q.** Median sclerite of genitalia. **R.** Endoparameral organ. **S.** Basimere and distimere. **T.** Ventral plate.

basitarsus 7.4 times as long as wide. Calcipala extending beyond middle of second tarsomere (fig. 130D). Basal tooth of claw medium size (figs. 130F, 178D). All abdominal sterna with simple hairs. Eighth sternite with gonapophyses and cercus as illustrated (fig. 130L); genital fork and spermatheca without special features.

Male. Length of wing 4.4–4.6 mm. Color as in female, but scutum dark reddish brown, in many specimens shoulders and sides anteriorly tending toward piceous, and abdominal tergites entirely dark except narrow posterior margin whitish.

Holoptic. Shape and proportions of antennal segments as in figure 130N; ratio length/width of first flagellomere 1:0.74. Apical segment of maxillary palp slightly longer than penultimate (fig. 130I). Second segment of maxillary palp abruptly narrowed on apical

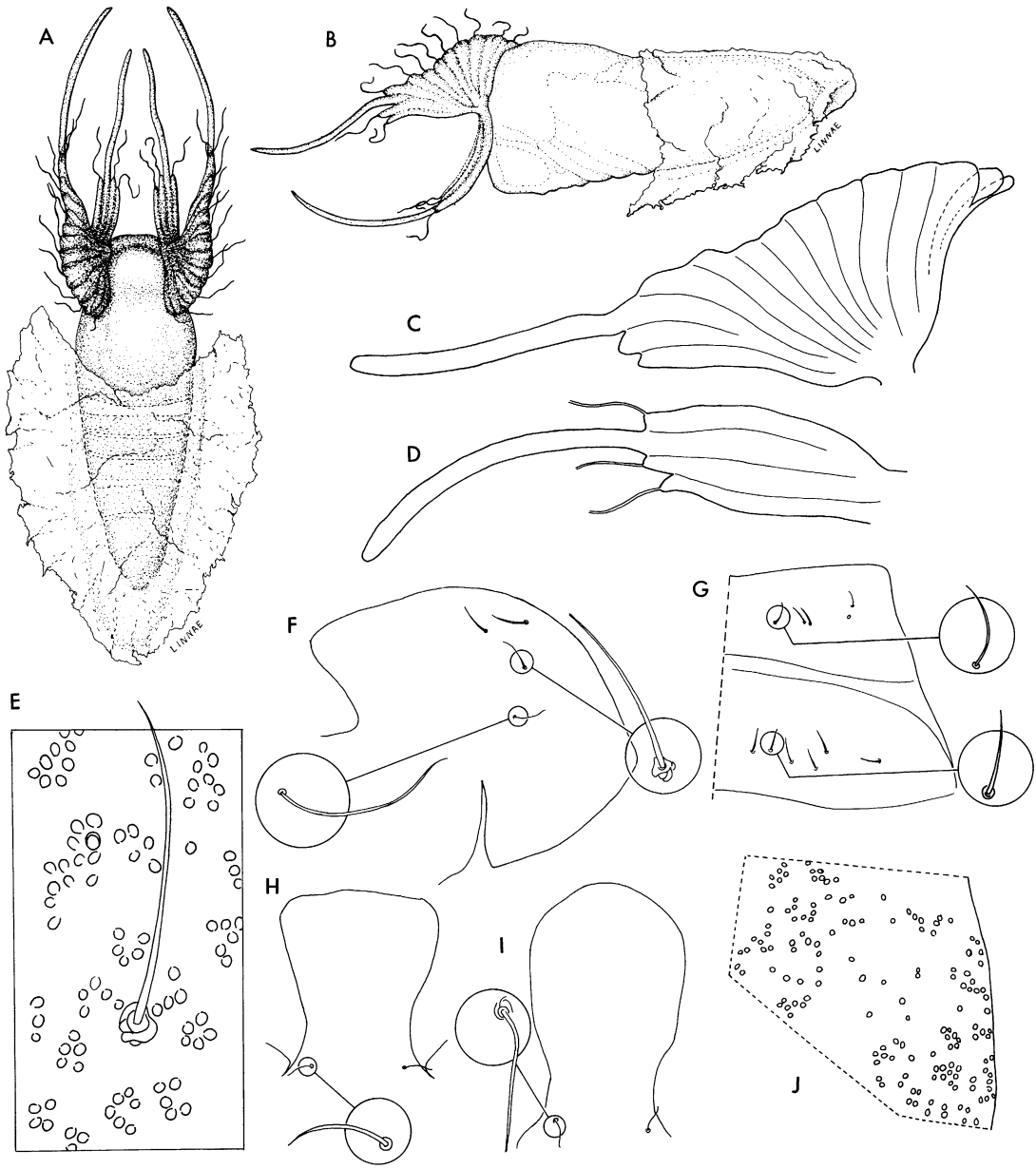

Fig. 131. *G. vulcanius.* Pupa. **A.** Pupa in cocoon, dorsal aspect. **B.** Same, side view. **C.** Upper section of gill. **D.** Lower section of gill. **E.** Detail of thorax, with platelets and trichome. **F.** Chaetotaxy of thorax. **G.** Chaetotaxy of abdominal tergites I and II. **H.** Outline of frontoclypeus of female. **I.** Same, male. **J.** Distribution of platelets of clypeus.

half. Sensory vesicle small, without distinct neck (fig. 130J). Chaetotaxy of wing as in female, but Sc only with 20–23 setae. Shape and proportions of fore and hind leg segments as shown in figure 130M, O. Fore basitarsus 10.7 times, hind basitarsus 6.9 times as long as wide. Calcipala very slightly surpassing middle of second tarsomere (fig. 130P). Distimere about two-thirds as long as basimere (fig. 130S). Main body of ventral plate as long

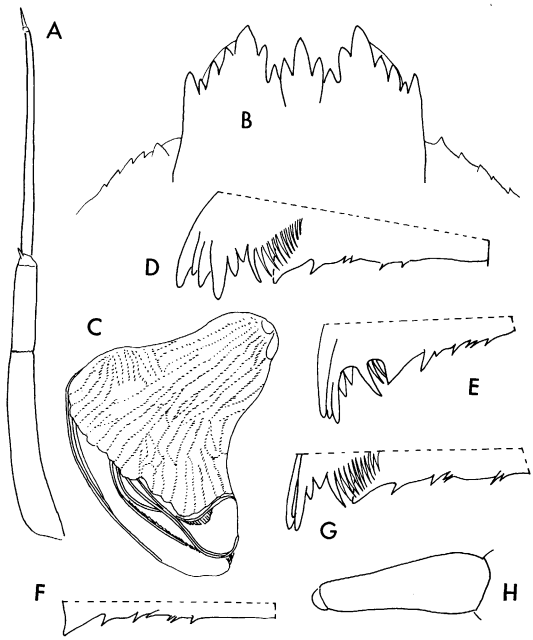

Fig. 132. *G. vulcanius.* Larva. **A.** Antenna. **B.** Anterior portion of hypostomium. **C.** Gill histoblast. **D-G.** Mandibular serrations and apical portion of mandible. **H.** Maxillary palp.

as wide (fig. 130T). Median sclerite and hooks of aedeagus as in figure 130Q, R.

Pupa. Cocoon covering pupa dorsally only to base of thorax, leaving most of thorax with gills and head uncovered (fig. 131A, B). Color of cocoon light brown, tightly woven, and slightly translucent. Length of cocoon along dorsum 3–4 mm. Total length of body of pupa 4.3–5.0 mm; cephalopterothecal length 2.9–3.0 mm. Gill with 18 branches fused into two shieldlike structures as in figure 131A–D. Dorsal shield formed by fusion of 1st to 14th branches, ventral shield by fusion of 15th to 18th. Areas of contact of branches indicated by lines of small perforations. Apices of components of shields angular or pointed, in some cases very slightly projecting beyond margin of shield. Twelfth and 16th branches elongate, projecting beyond margin of respective shield by length of same, their apices pointed or rounded. Apices of all branches (except 12th and 16th) with respiratory filaments. Surface of gill including free branches faintly wrinkled, without distinct cuticular processes. Shape and proportion of frontoclypeus of female and male pupae as shown in figure 131H, I; platelets few in number (fig. 131J), faintly verrucose, less numerous in male than in female. Facial trichomes in shape of slender setae. Platelets of thorax smooth, not numerous, in irregular groups as in figure 131E. Trichomes of thorax consisting of two slender, elongate submedian; and two very delicate hairlike dorsolateral setae (fig. 131F). Setae of tergite I very thin, hairlike, their length 85–100 μm; setae of tergite II as long as those of tergite I, slightly stronger (fig. 131G). Tergites III and IV each with 4 + 4 slender, apically drawn out hooks. Anterodorsal setae hairlike. Setae of tergites V–VIII slender, their length on tergite VII 85–95 μm. Spine-combs on tergites VI–VIII continuous on tergite VII with 30–35 spines, length not more than 20 μm, viz., one-fourth to one-fifth length of setae of this tergite. Specialized setae of eighth and ninth segments from almost straight to curved or twisted. Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 9.5–11 mm; width of head capsule 0.9–1.0 mm. Body shape as usual for genus; ventral papillae well developed. Color whitish, swollen posterior portion of body very faintly pigmented. Head light yellow; spots of cephalic apotome distinct. Hypostomial bridge lacking pattern elements. Antenna as long as stem of cephalic fan; first and second segments hyaline, third faintly pigmented. Shape of antenna as in figure 132A; ratio length/width of segments I–III = 1:0.45–0.5:1.2. terminal sensillum elongate, ratio length/width = 5. Cephalic fan with 30–35 rays, teeth slightly decreasing in size within each group of small teeth. Mandible (fig. 132D–G) with 10–12 inner teeth and 6–8 marginal serrations. Maxillary palp three times as long as wide at base (fig. 132H). Hypostomial teeth (fig. 132B) much as in *cormonsi*; 6–7 lateral serrations; 3–4 hypostomial setae in each row. Gill histoblast as in figure 132C. Perianal scales well developed, extending entire length of upper arms of X-shaped sclerite, but not forming complete rings. Anal armature with recurrent struts lo-

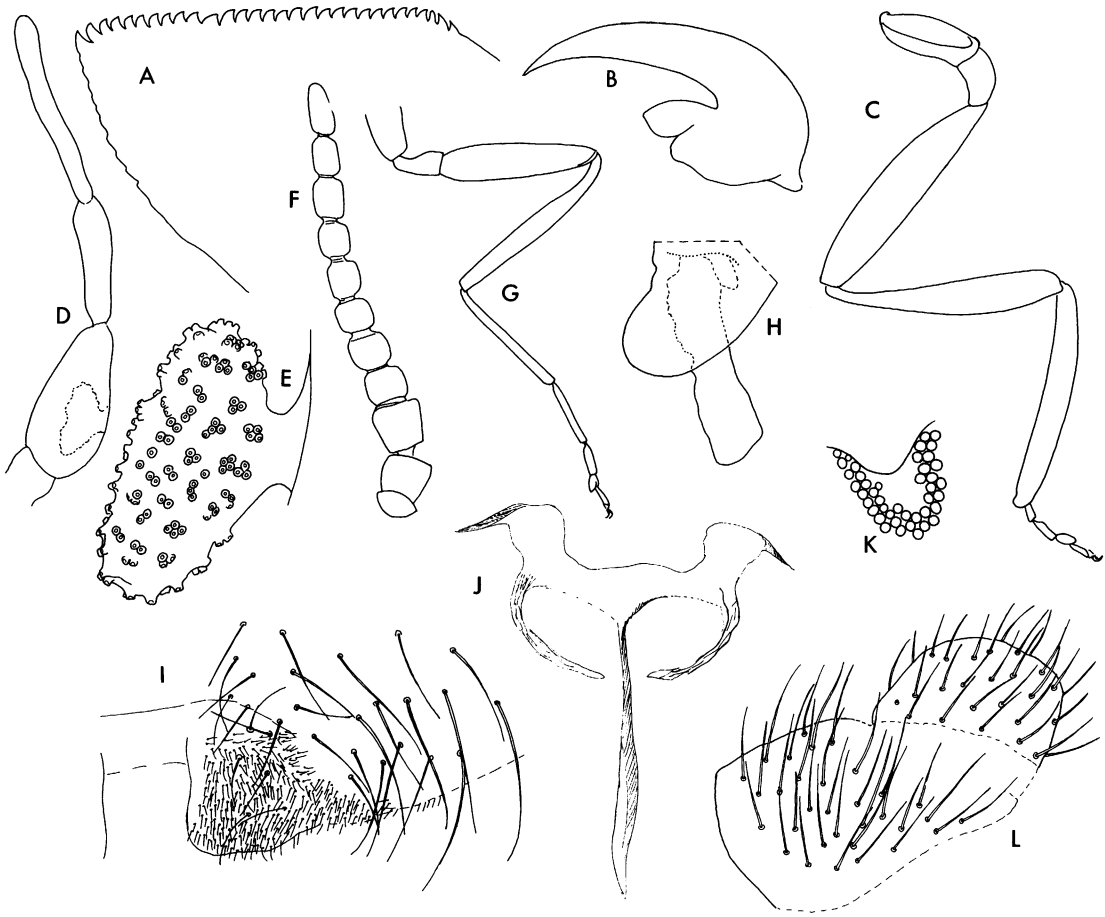

Fig. 133. *Gigantodax siberianus.* Female. **A.** Apex of mandible. **B.** Claw. **C.** Hind leg. **D.** Maxillary palp. **E.** Sensory vesicle of maxillary palp. **F.** Antenna. **G.** Foreleg. **H.** Calcipala and second tarsal segment. **I.** Portion of sternite VIII, with gonapophyses. **J.** Genital fork. **K.** Fronto-ocular triangle. **L.** Cercus and paraproct.

cally pigmented. Crochet ring with about 100 rows composed of 20–22 hooks each. Rectal gills not examined.

HOLOTYPE: ECUADOR: *Pichincha:* Quito-Papallacta road, 3300 m, July 20–Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female, allotype, 19 males, and 12 females, paratypes (reared, and with their associated pupal exuviae), pupae, 1 larva. ECUADOR: *Cotopaxi:* NW slope of Mt. Cotopaxi, 3500 m, July 26–Aug. 5, 1969 (P. and B. Wygodzinsky; AMNH), 9 males, 5 females, paratypes (reared, and with their associated pupal exuviae), pupae; Pujili-Quevedo road, Rio Sumbahua, 3500 m, July 29–Aug. 15, 1969 (P. and B. Wygodzinsky; AMNH), 1 pupa. *Charchi:* Paramo El Angel, Oct. 1969 (C. H. Perez; AMNH), pupae, larvae.

ETYMOLOGY: The specific name is from the Latin *vulcanius,* pertaining to volcanoes, in reference to the slopes of the volcano Cotopaxi, where a large population of this species was found.

BIOLOGY: The largest populations were found in slightly shaded irrigation ditches and small streams up to 30 cm wide and 10 cm deep, with temperatures around 10°C. The water was clear, with some organic matter

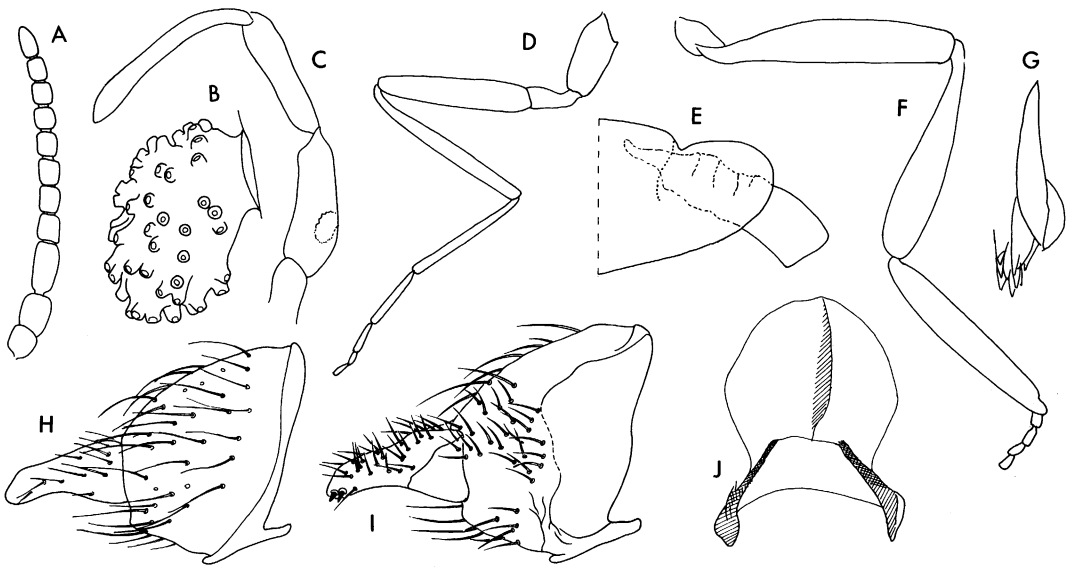

Fig. 134. *G. siberianus.* Male. **A.** Antenna. **B.** Sensory vesicle of maxillary palp. **C.** Maxillary palp. **D.** Foreleg. **E.** Calcipala and second tarsal segment. **F.** Hind leg. **G.** Endoparameral organ. **H.** Basimere and distimere, seen from below. **I.** Same, seen from above. **J.** Ventral plate.

deposited on the bottom of the watercourses and occasionally on the leaves where the specimens were found. Trailing grasses and the underside of watercress leaves were the preferred place of pupation. Frequently, two or three pupae were crowded together on the underside of one leaf; many, together with those of other species of *Gigantodax,* could be found on a single blade of grass.

DISCUSSION: The structure of the pupal gills of *vulcanius* agrees basically with that of the species of the *cormonsi* group. The large dorsal shield is formed by the fusion of the dorsal and lateral shields found in *cormonsi, praealtus, abalosi,* and *leonorum. Gigantodax vulcanius* shares with *G. siberianus* the comparatively long setae of the first abdominal tergite of the pupa; these setae are short in all other species of the complex. *G. vulcanius* is unique in the complex; the antenna of the larva is not perceptibly longer than the stem of the cephalic fan; in the remaining species of the complex the reverse is true.

Gigantodax siberianus, new species
Figures 133A–L, 134A–J, 135A–I, 136A–M

DIAGNOSIS: Differs from related species by the shape of the pupal gill with the branches forming three shields, none of which projects beyond the outlines of shields.

DESCRIPTION: *Female.* Length of wing 4.2–4.3 mm. Color as in *G. cormonsi* but abdominal hairs whitish. Frontal angle 50°. Frontoocular triangle slightly higher than wide (fig. 133K). Shape and proportions of antennal segments as shown in figure 133F. Mandible with 30–35 teeth (fig. 133A). Maxilla with about 28 teeth. Last segment of maxillary palp slightly longer than penultimate (fig. 133D). Second segment moderately elongate, ratio length/width = 1:0.47–0.49. Sensory vesicle large (fig. 133E) with distinct neck. Veins and setae of wings as in *cormonsi.* Shape and proportions of fore and hind leg segments as in figure 133C, G. Hind basitarsus 6.7–7.11 times as long as wide. Calcipala reaching middle of second tarsomere (fig. 133H). Basal tooth of claw subtriangular, comparatively small (fig. 133B). Abdominal sterna with delicate hairs only. Cercus, paraproct, genital fork, and eighth sternite with gonapophyses as shown in figure 133I, J, L.

Male. Length of wing 4.1–4.2 mm. Color as in female, but thorax rather dark reddish brown.

Holoptic. Shape and proportions of antennal segments as in figure 134A; ratio length/

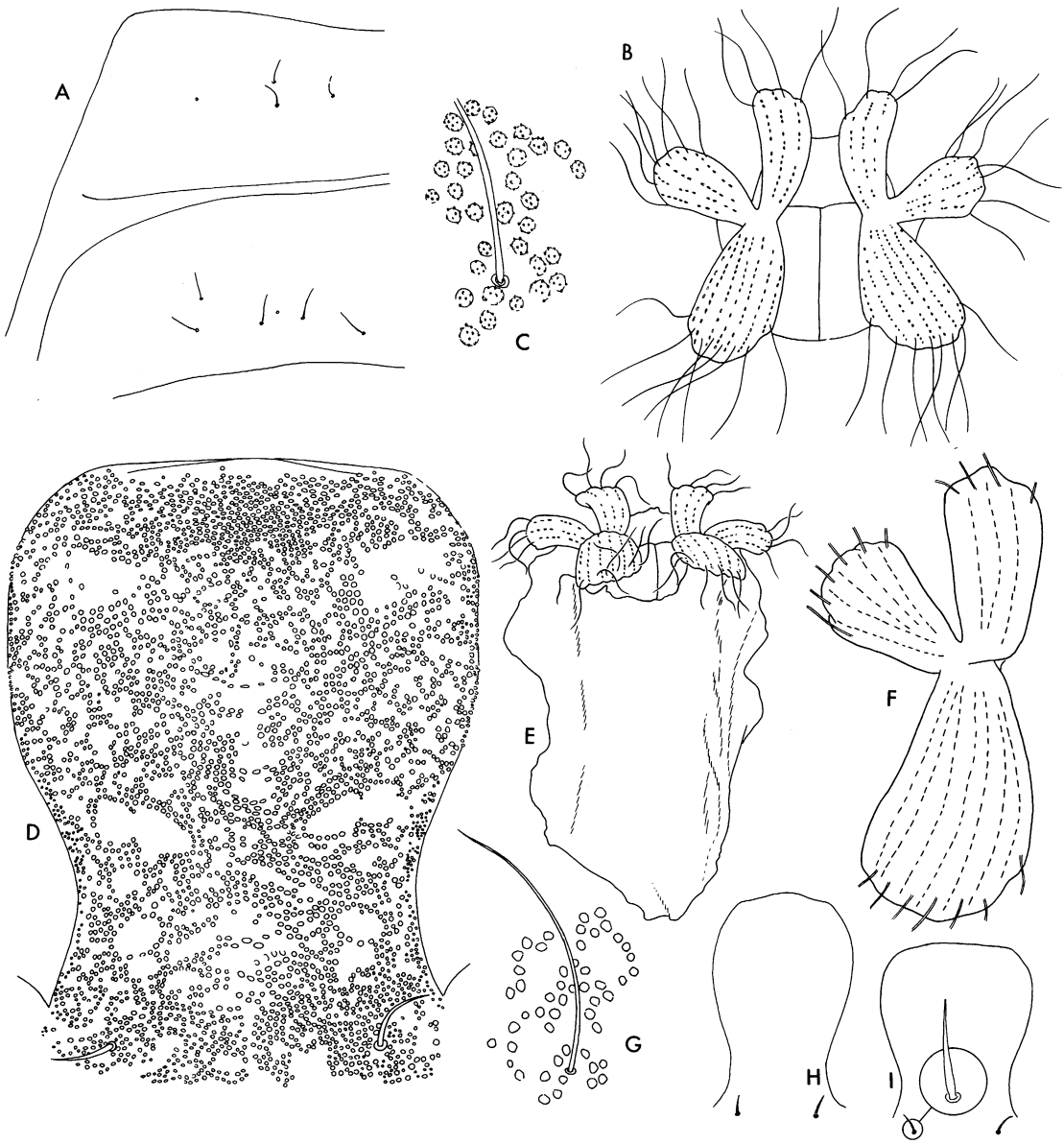

Fig. 135. *G. siberianus.* Pupa. **A.** Chaetotaxy of abdominal tergites I and II. **B.** Anterior portion of body with gills, frontal view. **C.** Detail of thorax, with platelets and sublateral trichome. **D.** Frontoclypeus of female. **E.** Pupa in cocoon, dorsal view. **F.** Gill. **G.** Detail of sublateral trichome of abdominal tergite III. **H.** Outline of frontoclypeus, male. **I.** Same, female.

width of first flagellomere 1:0.53–0.56. Shape of maxillary palp as in figure 134C. Sensory vesicle (fig. 134B) small, suboval, with very short neck. Wing as in female, but Sc with only about 20 hairs, and setae on R in a single row. Shape and proportions of fore and hind leg segments as in figure 134D, F. Fore basitarsus 14 times, hind basitarsus 5.8–5.9 times as long as wide. Calcipala extending slightly beyond middle of second tarsomere (fig. 134E). Genitalia as shown in figure 134G–J.

Pupa. Cocoon of irregular shape, extending

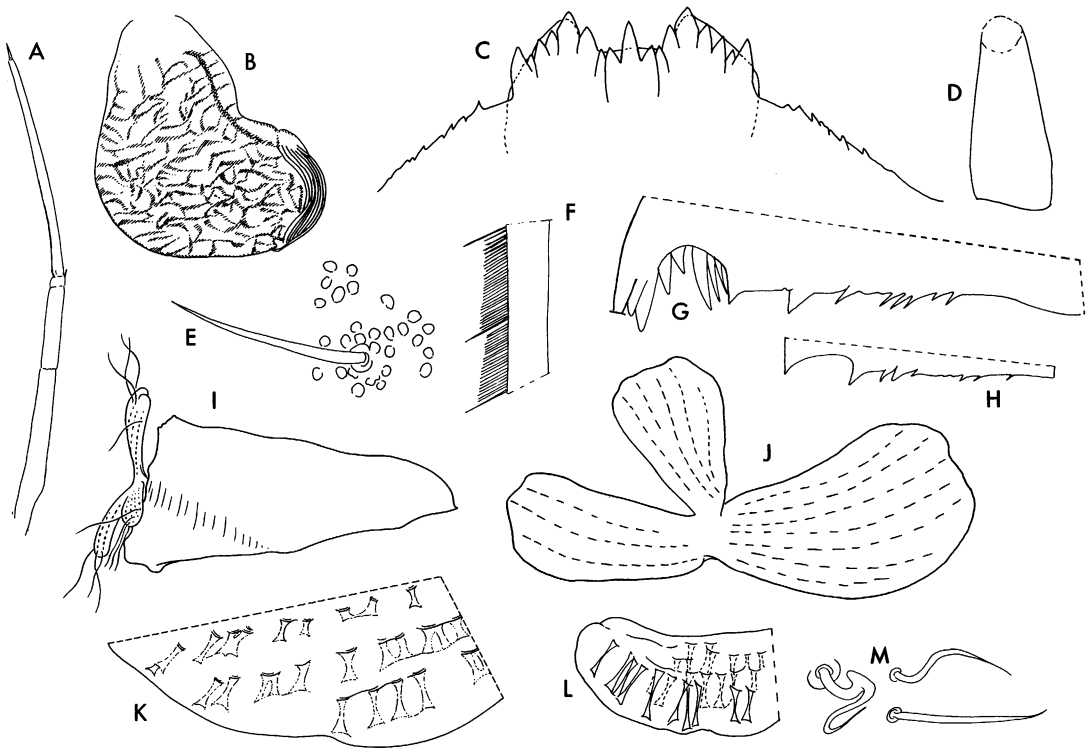

Fig. 136. *G. siberianus.* A–D. Larva. **A.** Antenna. **B.** Gill histoblast. **C.** Anterior portion of hypostomium. **D.** Maxillary palp. **E.** Submedian trichome of thorax of pupa. F–H. Larva. **F.** Teeth of ray of cephalic fan. **G.** Mandibular serrations and apical portion of mandible. **H.** Mandibular serration. I–M. Pupa. **I.** Pupa in cocoon, side view. **J.** Gill. **K, L.** Optical sections through gill clusters. **M.** Modified setae of sternite VIII.

dorsally to middle of thorax, laterally to level of insertion of gills; anterior portion of thorax, gills, and head free (fig. 135E, 136I). Color of cocoon light brown, tightly woven but translucent, frequently incrusted with foreign matter. Length of cocoon along midline dorsally 3.5–4.0 mm. Total length of body of pupa 4.3–4.7 mm; cephalopterothecal length 2.5–2.8 mm. Gill with 18 branches, fused into three shieldlike structures perpendicular to longitudinal axis of body (figs. 135B, E, F, 136I, J). Dorsal shield formed by fusion of 1st to 8th branches, lateral shield by fusion of 9th to 14th, and ventral shield by fusion of 15th to 18th; no branches projecting beyond border of shield. Area of contact of branches marked by line of perforation (figs. 135B, F, 136J–L). All branches with respiratory filaments inserted subapically. Cuticle of gills glabrous. Shape and proportions of frontoclypeus of female and male as in figure 135H, I, with numerous heavily verrucose platelets (fig. 135D). Facial trichomes short, slender, spinelike. Thorax with platelets of dorsal portion heavily verrucose, numerous, irregularly distributed (fig. 135C). Dorsocentral thoracic trichomes very slender, spinelike (fig. 135G); dorsomedian elongate, hairlike (fig. 136E). Setae of abdominal tergite I variable in length, 50–70 μm, delicate; setae of tergite II only slightly longer than those of I (70–80 μm) (fig. 135A). Tergites III and IV each with 4 + 4 short hooks drawn out into narrow points. Anterodorsal setae hairlike. Setae of tergites V–VIII slender, length on tergite VIII 80–90 μm. Spine-combs on tergites VI–VIII continuous or rarely interrupted at middle, consisting on tergite VII of 28–32 spines, their length 30–40 μm, viz., one-half to one-third the length of setae of this tergite. Specialized setae of eighth and ninth segments from straight to irregularly twisted

(fig. 136M). Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also on pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 8.7–9.5 mm; width of head capsule up to 0.9 mm. Body shape as usual for genus; ventral papillae well developed. Color of larva whitish; swollen posterior portion of abdomen somewhat darkened. Head yellowish. Spots of cephalic apotome small, distinct. Hypostomial bridge lacking pattern elements. Antenna slightly longer than stems of cephalic fan, very faintly pigmented. Shape of antenna as in figure 136A; ratio of segments I–III = 1:0.5–0.55: 1.1–1.25. Terminal sensillum elongate, about five times as long as wide at base. Cephalic fan with 20–24 large rays, their teeth as in figure 136F, distance between large teeth unusually great, small teeth only slightly decreasing in size within each group. Mandible (fig. 136G, H) with 8–9 inner teeth and 9–11 mandibular serrations. Maxillary palp 2.5 times as long as wide at base (fig. 136D). Hypostomial teeth (fig. 136C) much as in *G. cormonsi*; 7–10 lateral serrations; 3–4 hypostomial setae in each row. Cervical sclerites as in *G. cormonsi.* Gill histoblast as in figure 136B. Perianal scales inconspicuous, very few in number, restricted to area at base of X-shaped sclerite. Recurrent struts lightly pigmented distally. Crochet ring with 84–88 rows of 18–20 hooks each. Rectal gills not examined.

HOLOTYPE: COLOMBIA: *Cundinamarca:* Sitio Buenos Aires, near La Siberia, W of La Calera, 3050 m, July 17, 1967 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female, allotype, 3 males, 1 female, paratypes (reared, and with their associated pupal exuviae), pupae, and larvae; same, Aug. 26, 1969, 2 males, 1 female, paratypes (reared, and with their associated pupal exuviae), pupae; Bogota-Choachi road, 3250–3300 m, July 13, 1967 (P. and B. Wygodzinsky, AMNH), one pupa.

ETYMOLOGY: This species is named for the locality in the Colombian Andes near which most of the specimens were collected, La Siberia. This locality name is also found in other parts of western South America, and we hope it will not cause confusion.

BIOLOGY: The aquatic instars were collected in the lower reaches of the paramo formation, in a small stream (50 cm wide) and an irrigation ditch cutting through open land. Although the water was clear, considerable organic material was deposited on the bottom of the watercourses and on the grasses and other vegetation trailing in the water, where the larvae and pupae were collected. They occurred in the company of other species of *Gigantodax* and with *Simulium schmidtmummi,* a typical High Andes species from the area. The water temperature was 12°C.

DISCUSSION: *Gigantodax siberianus* belongs to the *cormonsi* group, with which it shares such synapomorphic characters as the highly specialized structure of the gills of the pupa (branches fused shieldlike) and the unusually elongate larval antenna (except *vulcanius*). The gills of *siberianus* differ from those of *cormonsi, abalosi, praealtus, leonorum,* and *vulcanius* by the complete absence of free branches; none projects beyond the margin of the shields formed by the fused branches. We believe this to be the most highly derived condition in this complex. Other characters that distinguish *siberianus* from the other species of the complex are, in the male, the unusually elongate first flagellomere and the presence of only a single row of setae on R. The pupa is distinguished, in addition to the structure of its gills, by the comparatively long setae of the first abdominal tergum, some of which are almost as long as those of the second tergite, but this character is also found in *vulcanius.* The larva of *siberianus* has a much smaller number of rays in the large mouth fan than the other species (20–24 versus 30 or more).

wrighti group

DIAGNOSIS: Recognized by a pupal gill with from 4 to 14 tubular or globose branches, frequently with membranous walls; subbasal clawtooth in females subtriangular; larva with median hypostomial tooth at or slightly above level of corner tooth (if below, then terminal antennal sensillum very elongate).

FEMALE: Medium orange brown to reddish brown. Morphology very close to *brophyi* group. Subbasal tooth of claw subtriangular (figs. 138L, 140F, 145N, 151D, 154P), in some specimens very elongate (figs. 157R,

174M, 178F), or nearly subrhomboidal in shape (figs. 143H, 159D). R_1 with spinules.

MALE: Morphology similar to *brophyi* group.

PUPA: Cocoon generally poorly developed. Gill reduced with from 4 to 14 terminal branches, with tubulose or globose shape, with short cuticular processes (figs. 141D, 144C), few respiratory filaments (fig. 168A, B, N) or membranous and wrinkled areas (figs. 146F, G, 149G, H, 155H, 172B–E). Trichomes of frontoclypeus and thorax hairlike (except *corniculatus* and *impossibilis*). Distal abdominal segment generally with specialized setae from curved to twisted (figs. 156E, 157P). Abdominal I generally with 5 + 5 trichomes of similar size. Terminal hooks stout.

LARVA: Cephalic apotome widest near base. Antenna generally as long as stem of cephalic fan, with terminal sensillum from moderately to distinctly elongated (ratio length/width = 1:4.0–8.0). Second antennal segment varying from about equal to one-third length of basal segment, but when short, terminal sensillum elongate; mandible with 9–11 marginal serrations; perianal scales varying from absent to forming a complete circumanal ring; recurrent struts generally well developed.

DISTRIBUTION: From Mexico to Tierra del Fuego (fig. 177).

DISCUSSION: This group possesses the most specialized pupal gills, showing reduction in the number of branches and respiratory filaments, and having the branches either tubular or globose, with a change of the wall structure from thick to membranous and wrinkled.

We recognize two subgroups. The first includes *horcotiani, bettyae,* and *septenarius* (and tentatively *conviti*), which have elongated hooks on pupal abdominal tergites III and IV (fig. 141J), presence of abundant respiratory filaments on the comparatively thin branches (figs. 139A–D, 141A–E, 144A–F), terminal sensillum of the larval antenna extraordinarily elongate [with a ratio of length/width over 6 (figs. 142G–I, 144H)] in conjunction with a very short second antennal segment (figs. 138T, 142A, B, 144G), and medium hypostomial teeth below level of corner teeth (figs. 138S, 142L, 144I). The third character is shared by the "*minor* group"; we consider it as a convergence.

The second subgroup has normal hooks on pupal abdominal tergites III and IV, the gill branches with few or no tegumentary processes, elongated, and inflated with membranous walls (figs. 146L, Q, T, 148C, D, 163A–C, 168A, B, N, 172B–E, 175A–D). Terminal sensillum and second segment of the larval antenna normal; and median tooth of hypostomium at the same level or above level of corner tooth. The last character is shared by *cortesi, igniculus,* and typical species of *cilicinus* groups, but here it is different because the fourth lateral teeth are below the level of the corner teeth. This subgroup includes *aquamarensis, cervicornis, corniculatus, wrighti, nasutum, rufescens, dryadicaudicis, incapucara, herrerus, impossibilis,* and *cypellus.*

Gigantodax horcotiani Wygodzinsky

Figures 138A–X, 139A–O

Gigantodax horcotiani Wygodzinsky, 1949: 326; 1951: 199; 1961a: 460; 1961b: 563. Vulcano, 1967: 3; 1977: 290.

DIAGNOSIS: Medium-size, reddish brown imagos, with scutum pigmented homogeneously, calcipala shorter than half the length of the second tarsomere, pupa with 12–14 tubular branches with cuticular processes and apically deciduous filaments, larva with median tooth as long as corner teeth and gill histoblast with thick branches and thin filaments.

REDESCRIPTION: *Female*: Length of wing 4.4–4.7 mm. Head including clypeus blackish, setae brass colored. Antenna and maxillary palp brown; scapus, pedicellus and base of first antennomere orange, only slightly larger than flagellum. Scutum light reddish brown, scutellum somewhat darker, metanotum piceous. Pleural region reddish brown. Thoracic setae brass colored. Wing translucent; veins light brown. Setae of stem vein and all other veins, dark. Halter light brown. Legs yellowish brown, hairs concolorous. Abdominal segments piceous, their hind borders narrowly whitish. Abdominal hairs brass colored.

Frontal angle 50–60°. Fronto-ocular tri-

angle about as high as wide (fig. 139D). Shape of antennal segments as in figure 139A. Mandible not examined in detail; teeth well developed. Maxilla with 24–26 teeth. Distal segment of maxillary palp almost twice as long as penultimate (fig. 138E). Second segment elongate oval, ratio length/width = 1: 0.53–0.56. Sensory vesicle medium-size, with distinct neck (fig. 138G). Wing similar to those of male (see below). Shape and proportions of fore and hind leg segments as in figure 138B, C; hind basitarsus about 9.5 times as long as wide. Calcipala not extending to middle of second tarsomere (fig. 138J). Basal tooth of claw as in figure 138L. Abdominal sterna with delicate hairs only. Eighth sternite and gonopophyses without special characters; genital fork and cercus incorrectly figured by Wygodzinsky (1951), but are shown as in figure 138H, M.

Male. Length of wing 4.0 mm. General color as in female, but clypeus light colored and scutum dark reddish brown.

Holoptic. Shape and proportion of antennal segments as in figure 138I; ratio length/width of first flagellomere 1:0.67–0.77. Terminal segment of maxillary palp twice as long as penultimate (fig. 138K). Sensory vesicle small, subglobular, with distinct short neck (fig. 138O). Sc with 20–22 setae. Setae on R arranged in two or three irregular rows. R_1 with setae in one or two rows on basal half; on apical half, setae in only one row, interspersed with spinules, the latter beginning approximately at level of insertion of Sc on C (fig. 138F); distal portion of R_1 only with spinules. R_s with setae on upper surface in one row, on undersurface in two to three rows. A_1 not reaching wing margin. Shape and proportions of fore and hind leg segments as in figure 138P, Q. Fore basitarsus 11.2–11.5 times, hind basitarsus approximately six times as long as wide. Calcipala approximately half the length of second tarsomere (fig. 138N). Genitalia (illustrated in detail in Wygodzinsky, 1949) without special characters; distimere about two-thirds the length of basimere, with two apical spines (fig. 138R); main body of ventral plate as long as wide.

Pupa. Cocoon small, only covering abdomen; thorax, head, and gills fully exposed. Color of cocoon brownish white, rather loosely woven, with individual threads distinguishable. Length of cocoon along dorsum 2 mm; cephalopterothecal length of pupa 2.5 mm. Gills each with 13 thick, tubular, distally narrowed branches of varied length (fig. 139A–C, I). Gill not heavily sclerotized, whitish, brown, their surface appearing polished; whole surface of branches minutely dotted, apical portion very faintly reticulated

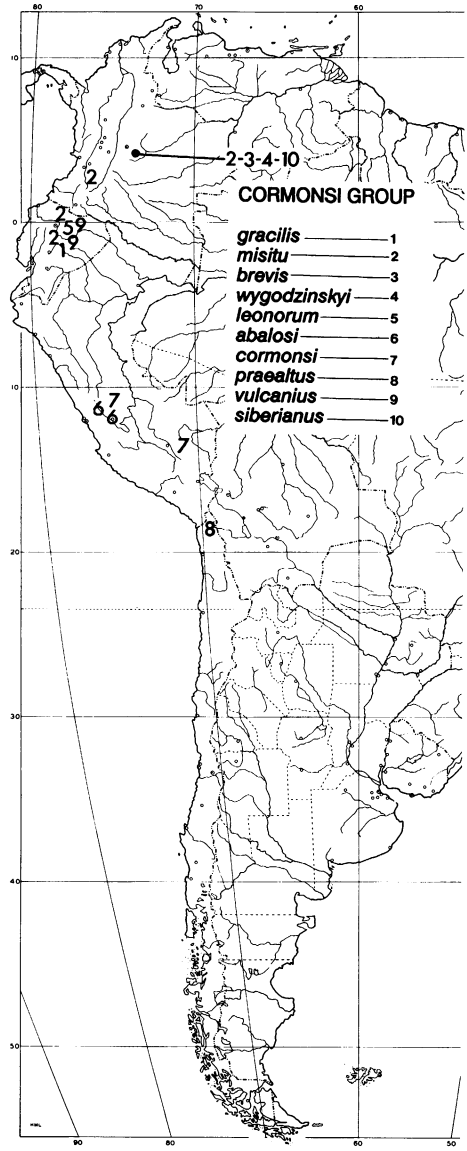

Fig. 137. Map with the distribution of species of *cormonsi* group.

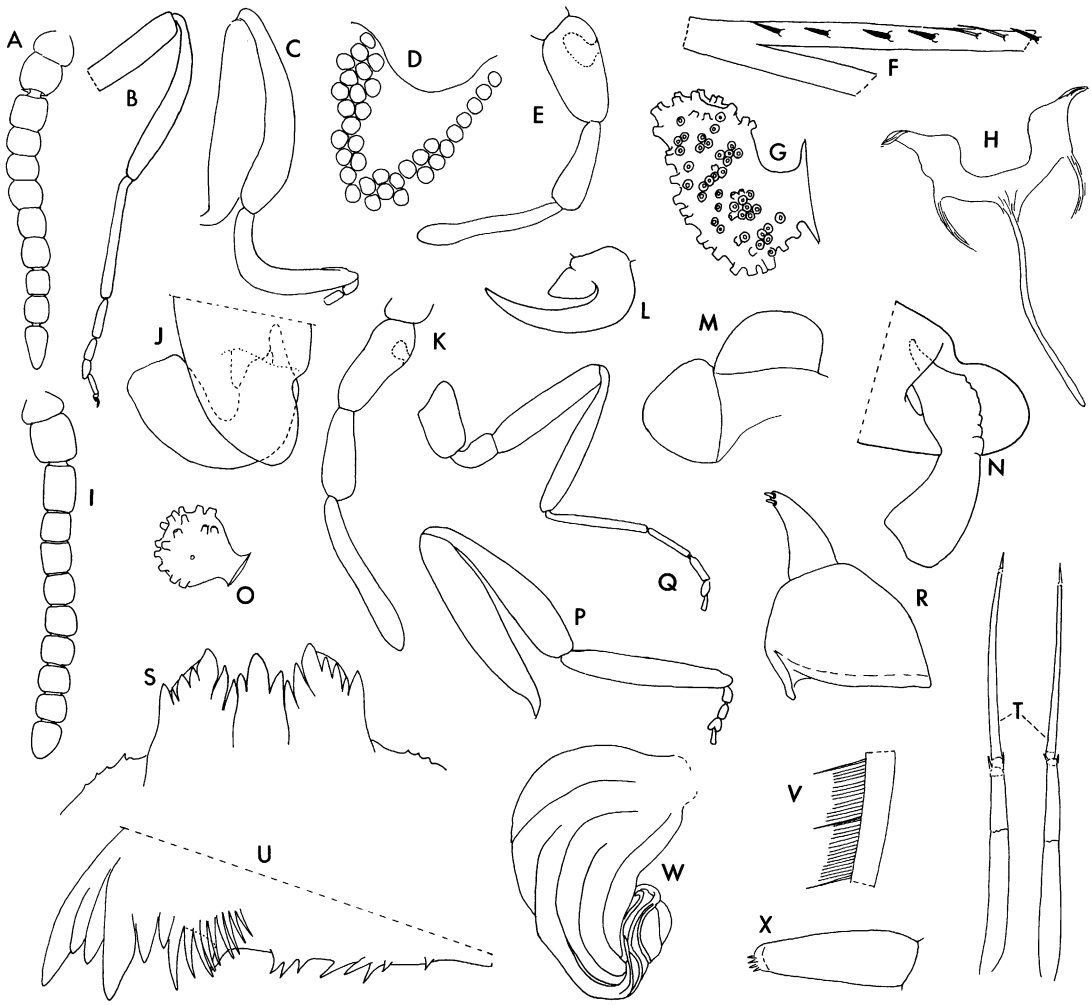

Fig. 138. *Gigantodax horcotiani.* A–H. Female. **A.** Antenna. **B.** Foreleg. **C.** Hind leg. **D.** Fronto-ocular triangle. **E.** Maxillary palp. **F.** Portion of wing. **G.** Sensory vesicle. **H.** Genital fork. **I.** Antenna, male. **J.** Calcipala, with second tarsal segment. **K.** Maxillary palp of male. **L.** Claw of female. **M.** Cercus and paraproct. N–R. Male. **N.** Calcipala, with second tarsal segment. **O.** Sensory vesicle of maxillary palp. **P.** Hind leg. **Q.** Foreleg. **R.** Basimere and distimere. **S.** Hypostomium. **T.** Antenna. **U.** Apex of mandible of larva. **V.** Teeth of rays of mouthfan. **W.** Gill histoblast. **X.** Maxillary palp of larva.

and with peglike cuticular processes (fig. 139D). Each branch apically with caducous respiratory filaments, best observed in gill histoblasts of pharate pupae. Length of gill branches extremely variable. First dorsal gill branch upwardly directed, simple, short, curved. Second and third branches upwardly directed, inserted on common trunk, fourth branch much longer than fifth. Sixth to ninth or tenth branches directed downward, on successive levels on short common trunk, in some cases branches reduced to short stubs (fig. 139I). Tenth to 12th or 11th to 12th branches directed downward, originating from comparatively long common trunk. Thirteenth branch directed downward, of medium length. Shape and proportions of frontoclypeus of female and male as in figure 139F, G, sclerite slightly rugose and with platelets less numerous in male (figs. 139H, L,); platelets conspicuously verrucose. Facial trichomes (fig. 139J) short, hairlike. Thorax

Fig. 139. *G. horcotiani.* Pupa. **A.** Gills, front view. **B.** Gill. **C.** Anterior portion of thorax, with gill, in side view. **D.** Distal portion of gill, with insertion of respiratory filament. **E.** Chaetotaxy of abdominal tergites I and II. **F.** Frontoclypeus of female pupa. **G.** Same, male pupa. **H.** Surface structure of clypeus, female. **I.** Frontal view of pupa, with gills. **J.** Facial trichome. **K.** Setae of distal segments of abdomen of pupa. **L.** Surface structure of clypeus, male. **M.** Dorsocentral trichome of thorax of pupa. **N.** Anterosublateral setae of abdominal tergite III. **O.** Hook of abdominal tergite III.

with platelets (fig. 139M) similar to those of frontoclypeus, irregularly arranged. Dorsocentral (fig. 139J) and dorsolateral trichomes hairlike, length of dorsocentrals 150 μm; dorolaterals more delicate than dorsocentrals. Setae of abdominal tergite I hairlike, very short, (30–40 μm), those of tergite II also hairlike (fig. 139E) but somewhat thicker at base and longer (45–55 μm). Tergites III and IV each with 4 + 4 long and very slender hooks (fig. 139O). Anterosublateral setae hairlike (fig. 139N). Setae of tergites VI–VIII minute, length about 20 μm. Spine-combs on tergites VI–VIII interrupted at center and oc-

casionally at other places; consisting on tergite VII of about 40 spines, with length about 20 μm, viz., as long as setae of this segment. Specialized setae of eighth and ninth segments straight or slightly curved, not branched (fig. 139K). Sternite V with 3 + 3, VI with 2 + 2, and VII with 1 + 1 long and slender hooks, similar to those on tergites III and IV; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 7.5–8.0 mm; width of head capsule 7.0–7.5 mm. Body shape as usual for the genus; ventral papillae well developed. Color of larva whitish, posterior region of body slightly darkened. Head very light brown; spots of cephalic apotome distinct but not dark. Hypostomial bridge lacking pattern elements. Antenna about as long as stem of cephalic fan; first and second segments hyaline, third somewhat darkened. Shape of antenna as in figure 138T; ratio of segments I–III = 1:0.33–0.36:1.26–1.34. Terminal sensillum slender, 6.0–6.3 times as long as wide at base. Cephalic fan with 33–35 large rays; teeth as in figure 138V. Mandible (fig. 138U) with 8 or 9 inner teeth and 9–10 marginal serrations. Maxillary palp three times as long as wide at base (fig. 138X). Hypostomium as in figure 138S. Median tooth below level of corner teeth apices, but beyond level of intermediate teeth apices; line connecting apices of corner teeth and fourth lateral teeth meeting at an angle of 100–110°. Hypostomium with lateral serrations and three or four hypostomial setae in each row. Cervical sclerites as in *G. cormonsi.* Gill histoblast as in figure 138W, its color brown in fully mature larva; respiratory filaments distinct. Perianal scales well developed, forming conspicuous circumanal ring. Recurrent struts well developed. Crochet ring with 80–88 rows of 16–18 hooks each.

MATERIAL EXAMINED: ARGENTINA: *Tucuman:* Tafi del Valle, 2000 m, Dec. 6–12, 1947 (R. Golbach; IML), 1 female. Specimens mentioned in former publications (Wygodzinsky, 1949, 1951) were examined again. *Jujuy:* Quebrada de Yala, Oct. 13, 1962 (S. Coscarón; MLP), several larvae. BOLIVIA: *Cochabamba:* Arroyo San Miguel, 3600 m, Nov. 17, 1977 (S. Coscarón; MLP), 1 pupa. The species was formerly known only from Tucuman.

BIOLOGY: The aquatic instars were found at Tafi del Valle at 2000 m elevation, on the undersurfaces of stones in a small, clear stream not over 1 ft wide and with very slow current.

DISCUSSION: The general structure of the gills of the pupa of *G. horcotiani* is similar to that found in *G. bettyae* and *septenarius.* The elongate hooks of the third and fourth abdominal tergites of the pupa, a synapomorphic character, are also shared by the three species. In some respects, *horcotiani* has more plesiomorphic characters as compared to the other two species: the gill branches of the pupa are not reduced in number and none are extremely elongate and extended backward over the body; the antenna of the larva is not distinctly longer than the stem of the cephalic fan, and the apical sensillum of the antenna is not quite as elongate.

Gigantodax bettyae Wygodzinsky

Figures 140A–U, 141A–K, 142A–S

Gigantodax bettyae Wygodzinsky, 1973: 246. Vulcano, 1981: 276. Ramirez Perez, 1983: 72.

DIAGNOSIS: Imagos reddish brown and without peculiar characters, larva also with distinctive characters, but pupa recognizable by the presence of nine gill branches having the apical portion rugose and with cuticular processes.

REDESCRIPTION: *Female.* Length of wing 3.8–4.3 mm, in most specimens between 4.0 and 4.3 mm. Head dark gray, setae brass colored. Antenna, maxillary palp, and clypeus light brown, scapus and pedicellus not much lighter than flagellum. Scutum light reddish brown, scutellum from stramineous to light brown, metanotum almost as dark as scutum. Pleural region reddish brown on upper, yellowish brown on lower half. Thoracic setae brass colored. Wing translucent; veins conspicuously yellowish brown, quite strongly colored even on posterior half of wing. Setae of stem black, with reddish tinge; setae of other veins black. Halter stem very faintly darkened, knob white. Legs yellowish brown, setae concolorous. Abdominal tergites piceous, their hind border narrowly whitish, posterior segments also on disc mottled with light color to a varied degree. Abdominal setae brass colored.

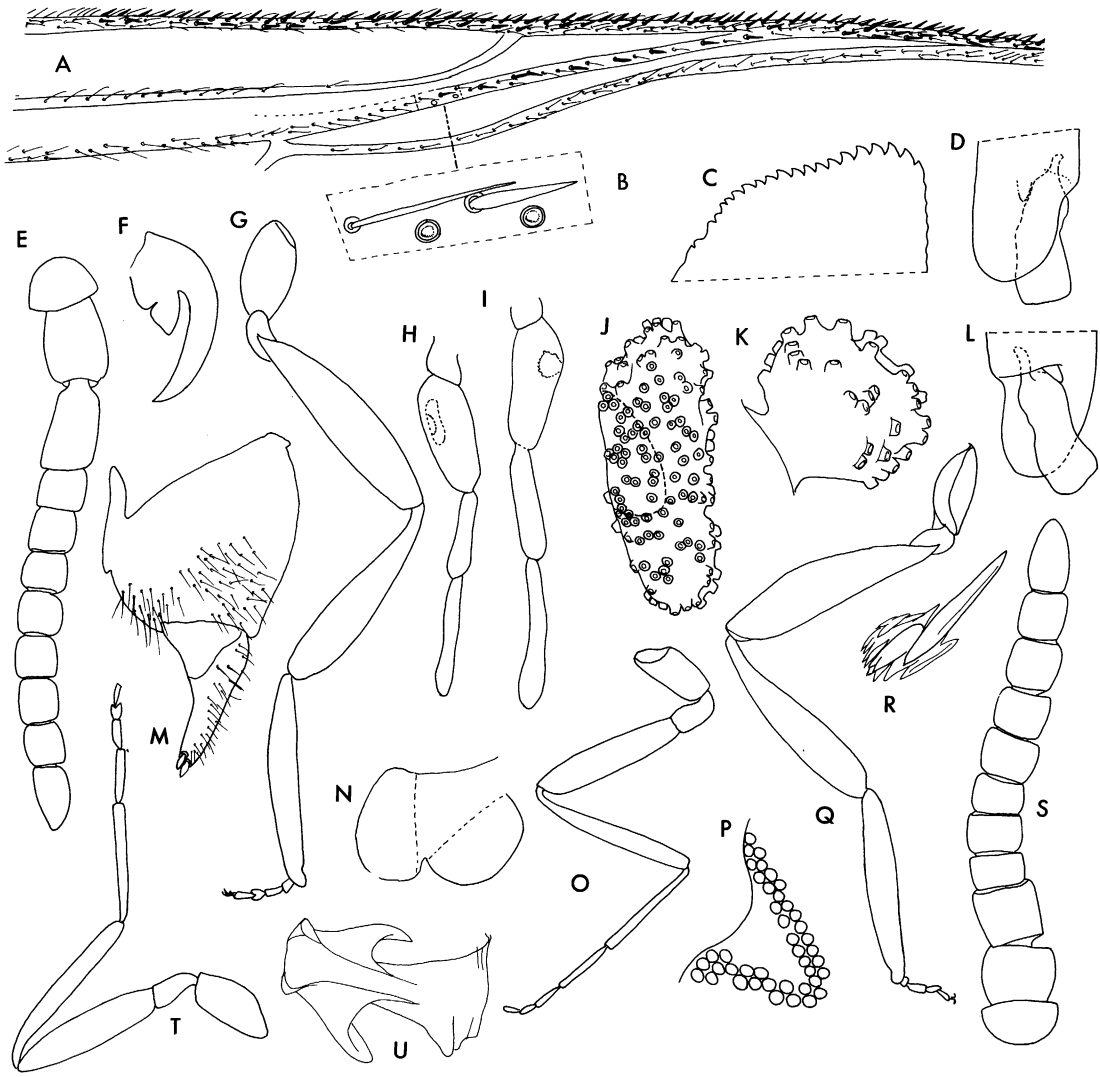

Fig. 140. *Gigantodax bettyae*. **A.** Portion of wing. **B.** Setae and spinules as found on R_1, with sensillae. **C.** Apex of mandible. **D.** Calcipala of female, with second tarsal segment. **E.** Antenna of male. **F.** Claw of female. **G.** Hind leg of female. **H.** Maxillary palp of female. **I.** Maxillary palp of male. **J.** Sensory vesicle of maxillary palp. **K.** Same, male. **L.** Calcipala of male. **M.** Basimere and distimere. **N.** Cercus and paraproct. **O.** Foreleg of male. **P.** Fronto-ocular triangle. **Q.** Hind leg of male. **R.** Endoparameral organ. **S.** Antenna of female. **T.** Forelegs of female. **U.** Median sclerite of male genitalia.

Frontal angle 55–60°. Fronto-ocular triangle slightly higher than wide (fig. 140P). Shape and proportions of antennal segments as in figure 140S. Mandible with 21–23 teeth; in some cases preapical portion of outer margin faintly crenulated (fig. 140C). Maxilla with 27–39 teeth. Distal segment of maxillary palp less than twice as long as penultimate (fig. 140H). Second segment elongate oval, ratio length/width = 1:0.45–0.49. Sensory vesicle large, with wide opening but without distinct neck (fig. 140J). Sc with 26–30 hairs. Setae on R arranged in two or three irregular rows. R_1 with one row of setae and spinules, the latter beginning at or slightly below level of insertion of Sc on C, spinules about as nu-

Fig. 141. *G. bettyae.* Pupa. **A.** Pupa and cocoon, dorsal view. **B.** Head and gills, frontal view. **C.** Pupa and cocoon, dorsal view, specimen different from A. **D.** Distal portion of gill branch. **E.** Pupa with cocoon, side view. **F.** Surface structure of clypeus, female. **G.** Same, male. **H.** Trichome of thorax of pupa. **I.** Chaetotaxy of I and II abdominal tergites. **J.** Hooks of tergites III–IV. **K.** Anterosublateral trichome of abdominal tergite III.

merous as setae. R_s with setae on convex portion in one row, on concave portion in two or three irregular rows. Shape and proportions of fore and hind leg segments as in figure 140T, G. Hind basitarsus 7.35–7.47 times as long as wide. Calcipala extending close to apex of second tarsomere (fig. 140D). Basal tooth of claw as in figure 140F. Abdominal sterna with delicate hairs only. Eighth sternite and genitalia without special characters; cercus and paraproct as illustrated (fig. 140N).

Male. Length of wing 3.5–3.8 mm. Color

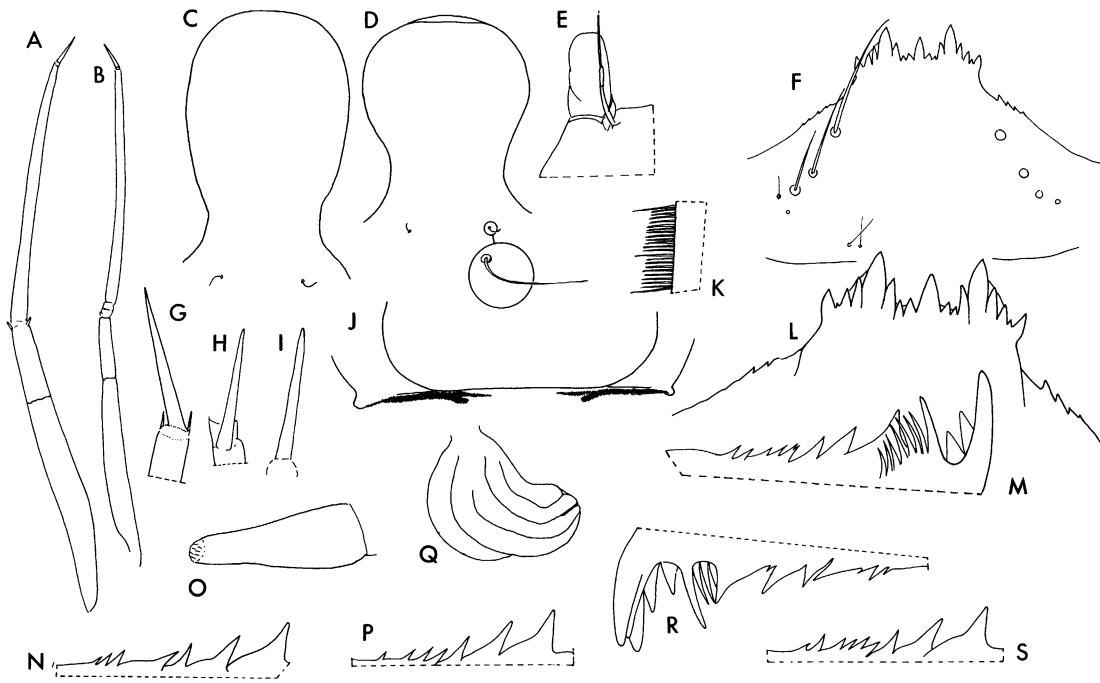

Fig. 142. *G. bettyae.* **A, B.** Antenna of larvae. **C.** Frontoclypeus of male pupa. **D.** Frontoclypeus of female pupa. E–S. Larva. **E.** Antenna and stem of cephalic fan. **F.** Hypostomium. **G–I.** Apical sensillum of antenna. **J.** Cervical sclerites. **K.** Teeth of ray of cephalic fan. **L.** Distal portion of hypostomium. **M, R.** Apex of mandible. **N, P, S.** Mandibular serrations. **O.** Maxillary palp. **Q.** Gill histoblast.

as in female, but reddish brown color of scutum darker, more saturated.

Holoptic. Shape and proportions of antennal segments as in figure 140E; ratio length/width of first flagellomere 1:0.53–0.67. Distal segment of maxillary palp slightly longer than penultimate (fig. 140I). Sensory vesicle (fig. 140K) small, subglobular, with short but distinct neck. Wing much as in female but Sc only with 15–17 setae. Shape and proportions of fore and hind leg segments as in figure 140O, Q. Fore basitarsus 11.7–13.0 times, hind basitarsus, 6.3–6.8 times as long as wide. Calcipala extending close to apex of second tarsomere (fig. 140L). Distimere about two-thirds as long as basimere, with two apical spines (fig. 140M); main body of ventral plate as long as wide; median sclerite and hook of endoparameral organ is in figure 140R, U.

Pupa. Cocoon small, covering only abdomen; thorax, head and gills free. Color of cocoon light brown, rather loosely woven with individual threads distinguishable, walls translucent. Length of cocoon along dorsum 2.1–2.5 mm. Total length of pupal body 3.9–4.1 mm; cephalopterothecal length 2.3–2.4 mm. Gills each with nine thick, tubular, distally slightly narrowed branches. First dorsal branch single, all others arising in pairs from short basal trunks. First dorsal branch subvertical; second and third extending backwards over dorsal portion of body; fourth and fifth extending along sides of body, sixth and seventh downward, and eighth and ninth downward and slightly forward (fig. 141A–C, E). Gills semirigid, whitish, their surface appearing polished. Basal portion of branches smooth, apical portion rugose and with peglike, microscopically dotted cuticular processes (fig. 141D). Apex of each branch with deciduous respiratory filament; filaments best observed in pharate pupae, detached in most free pupae. Shape and proportions of frontoclypeus of female and male as in figure 142C, D, with not very numerous poorly defined smooth platelets (fig. 141F, G). Facial trichomes very short, hairlike. Thorax with platelets similar to those of frontoclypeus,

viz., not numerous, smooth, many poorly defined (fig. 141H). Five to six dorsocentral and dorsolateral trichomes very short (90–110 μm), hairlike. Setae of abdominal tergite I hairlike, very short (20–30 μm), those of tergite II also hairlike but longer (35–55 μm) (fig. 141I). Tergites III and IV each with 4 + 4 long and very slender hooks (fig. 141J), anterosublateral setae hairlike (fig. 141K). Setae of tergites VI–VIII slender, length on tergite VII 50–70 μm. Spine-combs on tergites VI–VIII interrupted at center and occasionally at other sites, consisting on tergite VII of 29–31 spines, their length about 20 μm, viz., about one-third of length of setae of this tergite. Specialized setae of eighth and ninth segments straight or slightly curved, not branched. Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 long and slender hooks, similar to those of tergites III and IV; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 9.0–9.5 mm; width of head capsule 0.80–0.85 mm. Body shape as usual for the genus; ventral papillae well developed. Color of larva whitish, with dorsum darker, especially on swollen posterior portion of body; darkening due to faint but distinct hypodermal pigment. Head yellowish white; spots of cephalic apotome distinct. Hypostomial bridge lacking pattern elements, or very faintly darkened, with barely perceptible light-colored median longitudinal line. Antenna distinctly longer than stem of cephalic fan (fig. 142A–B); first and second segments hyaline, third distinctly pigmented. Shape of antenna as in figure 142A, B; ratio of segments I–III = 1:0.31–0.33:1.19–1.26. Terminal sensillum usually long and slender, eight times as long as wide at base (fig. 142G–I). Cephalic fan with 20–23 large rays; teeth as in figure 142K, small teeth subequal in size. Mandible (fig. 142M, N, P, R, S) with six to seven inner teeth and seven to nine marginal serrations. Maxillary palp three times as long as wide at base (fig. 142O). Hypostomium as in figure 142F, L. Median tooth falling short of level of corner tooth apex; line connecting corner teeth apices and fourth lateral tooth meeting at an angle of approximately 90°. Hypostomium with three to six (in most cases four to five) lateral serrations, and with two to four hypostomial setae in each row. Cervical sclerites as in figure 142J. Histoblast as in figure 142Q, with 5–9 visible branches, its color brown in fully mature specimens. Perianal scales forming complete circumanal ring, but largest and most heavily pigmented in dense group near upper arms of X-shaped sclerite. Recurrent struts well pigmented, unusually narrow and weakly pigmented distally. Crochet ring with 80–82 rows of 16–19 hooks each. Rectal gills not observed.

MATERIAL EXAMINED: VENEZUELA: *Merida:* southwest of Sucuruba, 2350 m, Feb. 9–26, 1960 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 male, holotype, 1 female, allotype, 17 males, 11 females, paratypes (all reared, and with associated pupal exuviae) pupae, and larvae.

BIOLOGY: This species was found only in one locality, in a small stream about a foot wide, flowing in grassland partially shaded by shrubs. The water was clear and its temperature was 17°, an unusually high water temperature for *Gigantodax.* Pupae were collected from the undersurfaces of watercress leaves, mostly singly, and from larger leaves originating from the shrubs shading the stream. Pupae were frequently found on the larger leaves, but never formed aggregations.

DISCUSSION: Females and males are similar to other species found in same area, such as *impossibilis, corniculatus, ortizi,* and *septenarius,* but the shape, number, and position of gill branches in the pupa are good characters to distinguish them from one another. *Gigantodax bettyae,* as is the case with *septenarius* and *horcotiani,* can be placed in the "*wrighti* group" only with difficulty, because of the hypostomial median tooth below the corner teeth, and the cuticular processes of the gill branches. They also possess a very elongate terminal article of the antenna, which we consider an apomorphic character. We therefore place them as a subgroup within the *wrighti* group.

Gigantodax septenarius, new species

Figures 143A–M, 144A–O

DIAGNOSIS: The species is easily recognized by a pupal gill composed of seven tubular branches arising individually from one basal trunk, except the second and third, which share a common trunk.

DESCRIPTION: *Female.* Length of wing 3.5–3.6 mm. Color as in *G. bettyae.* Frontal angle 45°. Fronto-ocular triangle about as high as wide at base. Shape and proportions of antennal segments as in figure 143C. Mandibles with 22–23 teeth on only inner margin. Maxilla with normal teeth, their number not established. Second segment of maxillary palp elongate oval, ratio length/width = 1:0.53. Sensory vesicle very large, with distinct neck (fig. 143A). Sc with 29–33 hairs. Setae of R in 2–3 irregular rows. Basal half of R_1 with setae in two irregular rows, on apical half in one row intermixed with spinules, the latter beginning at level of insertion Sc on C; spinules about as numerous as setae. R_1 with setae on convex portion of vein in one row, limited to apical half of vein, on concave portion setae in two or three irregular rows. Shape and proportions of segments of fore and hind legs as in figure 143E, J. Hind basitarsus 7.5 times as long as wide. Calcipala extending close to apex of second tarsomere (fig. 143L). Basal tooth of claw as in figure 143H. Abdominal sternites with delicate setae only. Eighth sternite and genitalia as in *bettyae.*

Male. Length of wing 3.6–3.65 mm. Color as in female, but scutum deep orange.

Holoptic. Approximate shape and proportions of segments of antenna as in figure 143D. Ratio length/width of first flagellomere not established. Sensory vesicle of maxillary palp small, subglobose, with short neck (fig. 143B). Wing much as in female, but setae on R and basal portion of R_1 in a single row. Shape and proportions of fore and hind leg segments as in figure 143G, I. Fore basitarsus 11.2 times, hind basitarsus 5.9–6.1 times, as long as wide. Calcipala extended well beyond center of second tarsomere (fig. 143F). Genitalia very close to *bettyae.* Distimere and basal plate as in figure 143K, M.

Pupa. Cocoon extremely small, covering abdomen ventrally to tip of pterothecae but dorsally only to and including fourth tergite (fig. 144A, B, D). Color of cocoon brownish white, rather loosely woven with individual strands perceptible, translucent. Length of cocoon about 2 mm. Total length of body of pupa 4.5 mm; cephalopterothecal length 2.5 mm. Gill semirigid, each with seven thick, tubular, apically pointed branches (fig. 144A–D, F). Gill branches not heavily pigmented, whitish, surface appearing polished under low magnification. Entire surface of branches, except extreme base, delicately reticulate (fig. 144C) and with peglike, microscopically dotted cuticular processes (fig. 144E). Each branch apically with caducous respiratory filaments (not shown in illustration). First dorsal branch subvertical; second and third extending backward over dorsal surface of pupa, the remaining along sides of pupa. Frontoclypeus of male and female and thorax with

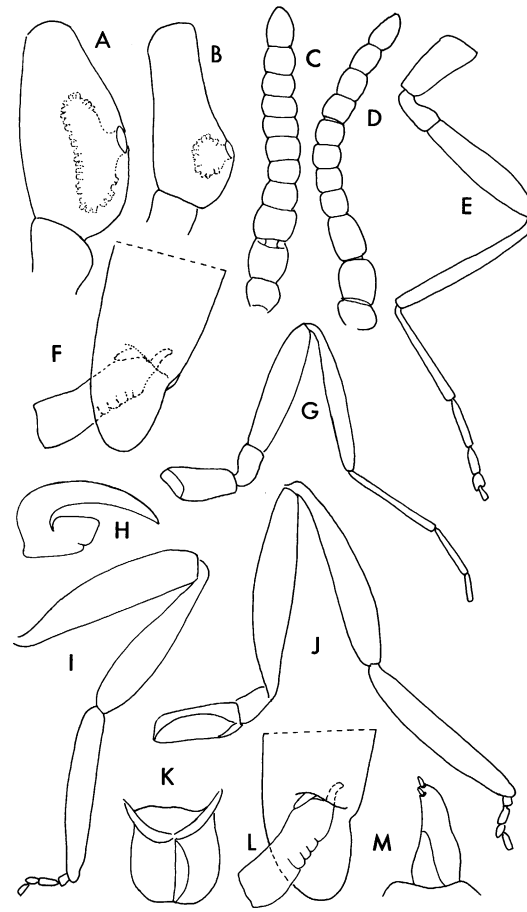

Fig. 143. *Gigantodax septenarius.* **A.** Second segment of maxillary palp of female, with sensory vesicle. **B.** Same, male. **C.** Antenna of female. **D.** Antenna of male. **E.** Foreleg, female. **F.** Calcipala of male, with second tarsal segment. **G.** Foreleg of male. **H.** Claw of female. **I.** Hind leg of male. **J.** Same, female. **K.** Ventral plate. **L.** Calcipala of female, with second tarsal segment. **M.** Distimere.

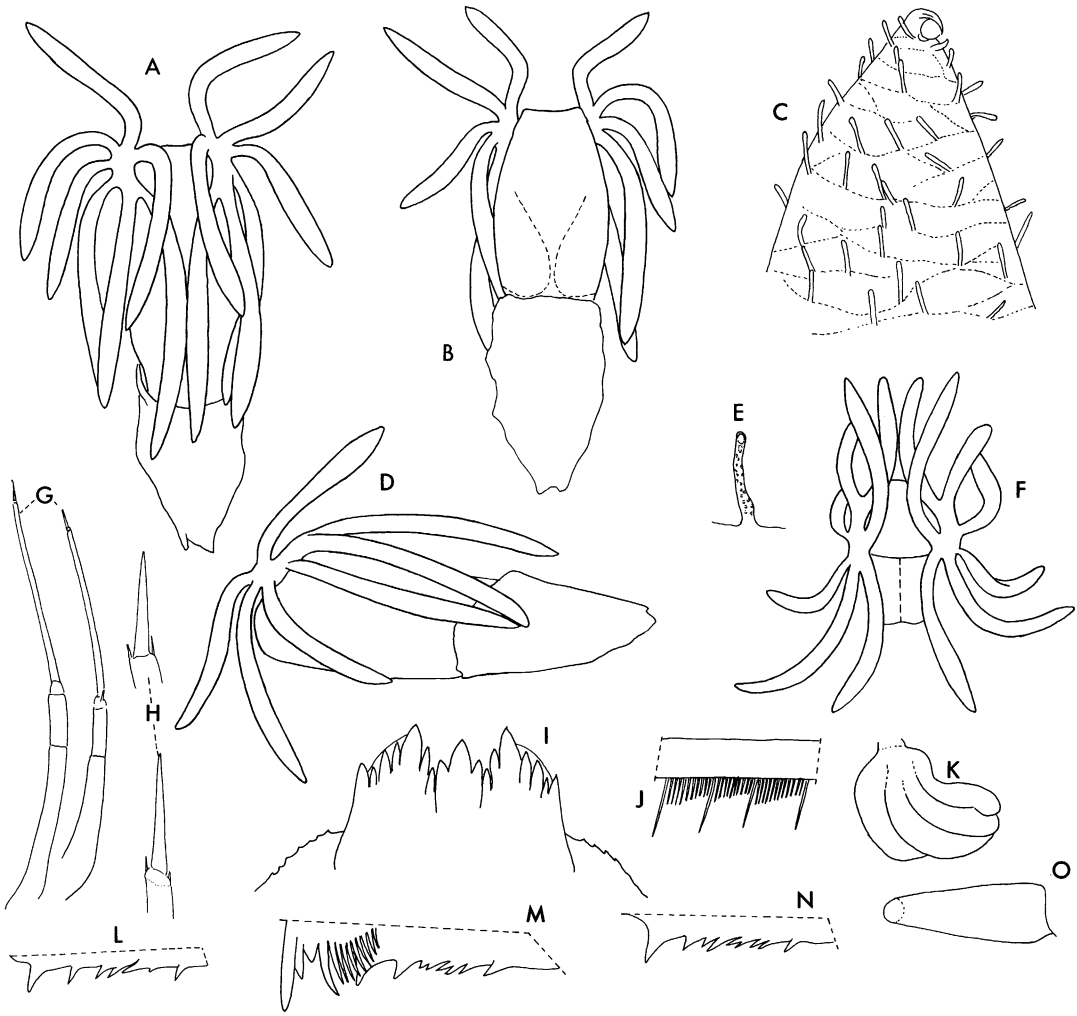

Fig. 144. *G. septenarius.* A–F. Pupa. **A.** Pupa in cocoon, dorsal aspect. **B.** Same, ventral view. **C.** Apex of gill branch, high magnification. **D.** Pupa in cocoon, side view. **E.** Processes of cuticula of gill branches. **F.** Head with gills, frontal view. G–O. Larva. **G.** Antenna. **H.** Apical sensillum of antennae. **I.** Anterior portion of hypostomium. **J.** Details of teeth of rays of cephalic fan. **K.** Gill histoblast. **L.** Mandibular serrations. **M.** Mandibular serrations and apex of mandible. **N.** Mandibular serrations. **O.** Maxillary palp.

their platelets and trichomes as in *bettyae.* Onchotaxy of abdomen, including measurements, as in *bettyae.*

Mature larva. Length 8.5 mm, width of head capsule 7.5 mm. Body shape as usual for genus; ventral papillae well developed. Color of larva light brown, due to uniformly distributed hypodermal pigment. Head yellowish white; spots of cephalic apotome distinct. Hypostomial bridge lacking pattern elements. Antenna distinctly longer than stem of cephalic fan. First and second segments almost hyaline, third distinctly pigmented. Shape of antenna as in figure 144G; ratio of segments I–III = 1:0.3:1.0–1.1. Terminal sensillum unusually long and slender, 7.5 times as long as wide at base (fig. 144H). Cephalic fan with 30–33 large rays, teeth as in figure 144J. Mandible (fig. 144L–N) with 9–10 inner teeth and 7–9 marginal serrations. Maxillary palp three times as long as wide at base (fig. 144O). Hypostomium as in figure 144I; general structure as in *G. bettyae;* with 5–9 lateral serrations and 3–4 hypostomial

setae in each row. Cervical sclerites as in *bettyae.* Gill histoblast as in figure 144K; with four visible branches, brown in fully mature specimens. Perianal scales feebly pigmented and very few in number, forming small, loose group near upper arms of X-shaped sclerite, not forming perceptible circumanal ring. Recurrent struts well pigmented, not unusually narrow. Crochet ring with about 90 rows of 17–20 hooks each.

HOLOTYPE: COLOMBIA: *Cundinamarca:* 2 km SW of Alban, 2400 m, Aug. 6–7, 1967 (P. and B. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female, allotype, 1 female paratype (reared, and with their associated pupal exuviae), pupae, and larva; ibid., Aug. 24, 1969 (P. and B. Wygodzinsky; AMNH), 3 males, 1 female, paratypes (reared, and with their associated pupal exuviae), 1 pupa, larvae.

ETYMOLOGY: The specific name is taken from the Latin *septenarius,* consisting of seven, referring to the seven-branched gills of the pupa.

BIOLOGY: The species was taken in one location, a stream from 1 to 2 ft wide, with a water temperature of 15–17°C, in open grassland. Pupae were located on the undersurfaces of stones lying in the stream.

DISCUSSION: *Gigantodax septenarius* is very close to *G. bettyae* with which it shares, among other characters, such synapomorphic features as the general structure of the pupal gill, and the unusually elongate terminal sensillum of the larval antenna. The female of *septenarius* can be easily distinguished from that of *bettyae* by the much larger sensory organ of the maxillary palp. The male of *septenarius* differs from that of *bettyae* by its orange scutum (reddish brown in *bettyae*). The pupae differ by the number of branches and the somewhat different integumental structure of the gill. The larvae of the two species are very similar.

Gigantodax conviti Ramirez Perez

Gigantodax conviti Ramirez Perez, 1980: 53; 1983: 72.

DISCUSSION: *Gigantodax conviti* was described from female, male, and pupal specimens take at 2350 m at Merida, Venezuela. We were unable to examine this material, but from the description and illustrations, this species is close to, but not the same as, species of the *wrighti* group. In accordance with the pupal gill, it is very close to *G. septenarius,* but that species has thinner branches; also, there are differences in the female claws and ventral plate of the male. We therefore prefer to retain *conviti* as a separate species.

Gigantodax aquamarensis De Leon

Figures 145A–O, 146A–V

Simulium aquamarensis De Leon, 1945: 72.
Gigantodax aquamarensis: Dalmat, 1951: 50. Dalmat, 1955: 102. Vulcano, 1967: 2.

DIAGNOSIS: Very close to *wrighti* in imago and larva but the 13–14 tubular gill branches of the pupa permit their differentiation.

REDESCRIPTION: *Female.* Length of wing 3.4–3.5 mm. Color as in *wrighti.* Frontal angle approximately 55°. Fronto-ocular triangle wider than high (fig. 145A). Shape and proportions of antennal segments as in figure 145B. Mandible with approximately 22 teeth. Maxilla with 22–24 teeth. Distal segment of maxillary palp not examined; second segment shortly suboval (fig. 145D) ratio length/width = 1:0.65. Sensory vesicle (fig. 145C) large, with short neck. Sc with 10–12 setae. R with setae in a single row, only occasionally setae arranged in pairs; setae not distinctly clustered at junction of R and R_1. R_1 with setae in one row on basal half, in two irregular rows on apical half, interspersed with spinules, the latter beginning basad of level of insertion of Sc on C; spinules less numerous than setae. R_s with setae in one row on upper, and one to two rows on lower surface. A_1 not reaching wing margin. Hind leg as in figure 145E. Hind basitarsus 7.2 times as long as wide. Calcipala well beyond middle of second tarsomere (fig. 145I). Basal tooth of claw small (fig. 145N). Abdominal sternites with only delicate hairs. Genitalia without special characters. Genital fork not heavily pigmented (fig. 145F). Paraproct short (fig. 145M).

Male. Length of wing 3.2–3.4 mm. Color as in *wrighti.* Holoptic. shape and proportions of basal antennal segments as in figure 145K; ratio length/width of first flagellomere 1:0.57. Second segment of maxillary palp and sensory vesicle as in figure 145H. Shape of hind leg segments as in figure 145O. Hind basitarsus 6.3 times as long as wide. Calcipala

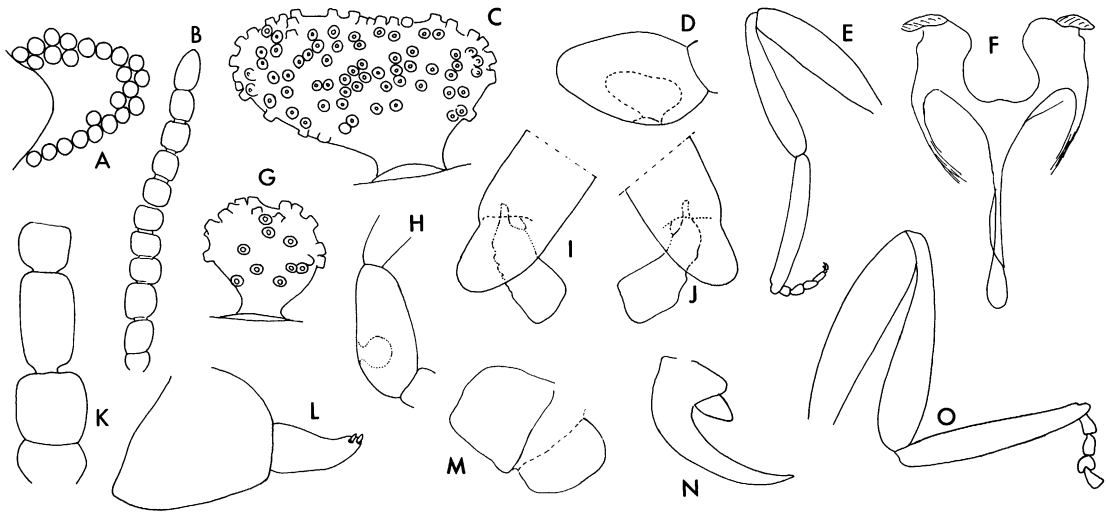

Fig. 145. *Gigantodax aquamarensis.* A–F. Female. **A.** Fronto-ocular triangle. **B.** Antenna. **C.** Sensory vesicle of maxillary palp. **D.** Second segment of maxillary palp, with sensory vesicle. **E.** Hind leg. **F.** Genital fork. **G.** Sensory vesicle of male. **H.** Second segment of maxillary palp. **I, J.** Calcipala with second tarsal segment. I. Female. J. Male. **K.** Base of antenna of male. **L.** Basimere and distimere. **M.** Cercus and paraproct. **N.** Claw. **O.** Posterior leg of male.

(fig. 145J) well beyond center of second tarsomere. Distimere only slightly longer than half the length of basimere, with two apical spines.

Pupa. Cocoon baglike, covering entire abdomen of pupa, but leaving thorax, head, and gills exposed. Color of cocoon dark brown. Cephalopterothecal length 2.3–2.4 mm. Gills semirigid, with 13, rarely 14, tubular branches forming a compact bundle (fig. 146L, Q, T). Gills with five or six primary branches: two dorsal, two or three lateral, and one ventral. Inner dorsal branches and ventral branch simple; outer dorsal branch divided at or beyond middle into two secondary branches; sublateral arms with two to four secondary branches. Branches gradually tapering toward apex, distally with caducous respiratory filaments. Surface of branches wrinkled as in figure 146F; cuticular projections absent. Frontoclypeus of female as in figure 146S, that of male similar but narrower; platelets as in *wrighti.* Facial trichomes hairlike (fig. 146R). Thorax with regularly spaced glabrous, or very faintly verrucose platelets (fig. 146U). Dorsocentral and dorsolateral trichomes hairlike. Setae of abdominal tergite I hairlike (fig. 146P), length 65–85 μm; setae of abdominal segment II spinelike, length 25–35 μm. Tergites III and IV each with 4 + 4 hooks; anterodorsal setae spinelike (fig. 146V). Setae of tergites V–VII very short, length on VII 35–40 μm. Spine-combs on segments VI–VIII continuous or with irregular interruptions consisting on tergite VII of 23–26 spines, their length 18–20 μm, viz., half as long as setae of this segment. Specialized setae of segments VIII and IX variously bent but not branched. Sternite IV with short hooklike setae arranged in three pairs. Sternite V with 3 + 3, VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. 6.8–7.5 mm; width of head capsule approximately less than 0.7 mm. Shape of larva as usual for the genus; ventral papillae small but perceptible in well-preserved specimens (fig. 146K). Overall color whitish, tinged rather uniformly with light violaceous hypodermal pigment, absent only on undersurface of widened posterior portion of body. Head light brown, with pattern of cephalic apotome almost imperceptible. Hypostomial bridge not darkened. Antenna slightly shorter than stem of cephalic fan (as

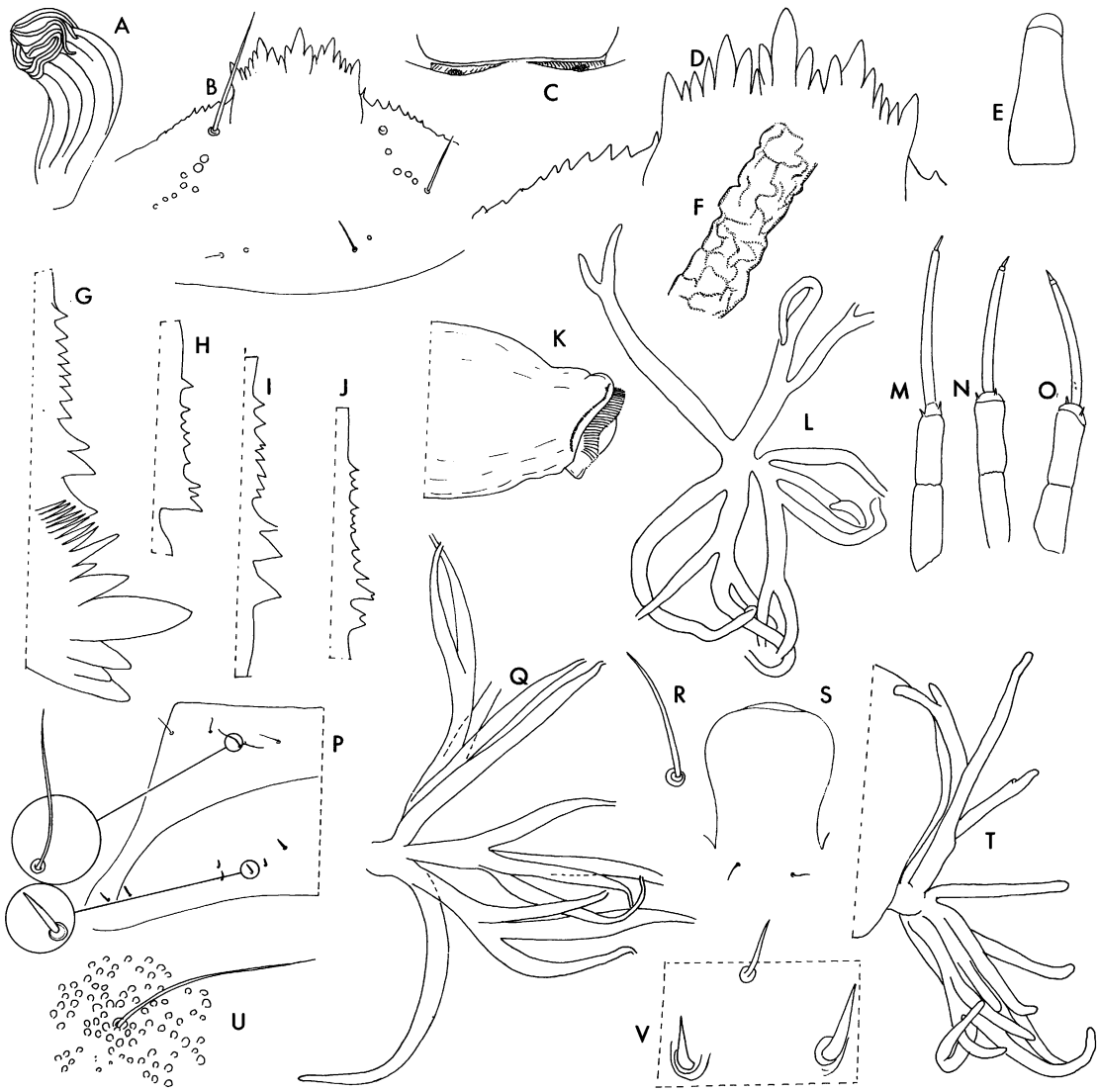

Fig. 146. *G. aquamarensis.* A–K. Larva. **A.** Gill histoblast. **B.** Hypostomium. **C.** Cervical region. **D.** Anterior portion of hypostomium. **E.** Maxillary palp. **F.** Surface structure of terminal portion of gill branches. **G.** Apex of mandible. **H–J.** Mandibular serration. **K.** Terminal portion of body of larva, side view. **L.** Gill of pupa, in slide mount. **M–O.** Antennae of larvae. P–V. Pupa. **P.** Chaetotaxy of abdominal tergites I and II. **Q.** Gill. **R.** Facial trichome of pupa. **S.** Frontoclypeus of female. **T.** Different gill. **U.** Thoracic trichome. **V.** Hooks of abdominal tergite III.

in *wrighti*), pigmented, third segment darker than the two preceding. Shape of antenna as shown in figure 146M, N, O; ratio of segments I–III = 1:0.79–1.04:1.82–2.17. Terminal sensillum approximately five times as long as wide at base. Mandible (fig. 146G–J) with 9–10 inner teeth and 10–13 marginal serrations. Maxillary palp about 2.5 times as long as wide at base (fig. 146E). Hypostomium as in figure 146D. Median tooth beyond level of corner tooth apex; line connecting apex of median tooth to apex of fourth lateral tooth intersecting corner tooth; 6–8 hypostomial setae and 9–11 lateral serrations. Cervical sclerites as in figure 146C. Gill histoblast as in figure 146A, piceous in fully mature

specimens, characterized by five or six perceptible main branches. Perianal scales absent. Anal sclerite with well-developed, wide recurrent struts. Crochet ring with 105–120 rows of 22–25 hooks.

MATERIAL EXAMINED: The specimens on which the above redescription is based are those seen by Dalmat (1955), collected in Guatemala at Aguas Amargas, Zunil, in the department of Quezaltenango. The species has not been reported from any other locality, notwithstanding the very intensive collecting evident from Dalmat's (1955) report.

BIOLOGY: De Leon (1945) found aquatic instars in streams with high mineral content. Larvae were adhering in enormous numbers to rocks and plants in the stream bed; aggregations of pupae were found in rock depressions. Dalmat (1945) gave more detailed information on the habit of this species, which he considered as zoophilic. It is found only about 6000 ft, in streams of a depth from 1 inch to 1 ft, and from 3 to 8 ft wide. These streams were invariably highly acidic, with a pH of 5; no other insect life was encountered. Dalmat observed pupation to be on stones only because he did not encounter any plant life.

DISCUSSION: Dalmat's (1955) redescription and keys contain several minor inaccuracies, which are rectified in our redescription. We draw special attention to the fact that the larvae of *aquamarensis* do not possess ventral papillae; Dalmat (1955) thought they were absent.

We believe *aquamarensis* to be close to *wrighti,* with which it agrees in the general structure of the adult, pupa, and larva, as can be seen in our descriptions and illustrations. The main differences between the larvae and pupae of the two species are shown in the keys; the adults may be very difficult to separate, though *aquamarensis* is somewhat smaller.

Gigantodax cervicornis Wygodzinsky

Figures 147A–Q, 148A–L, 149A–K, 150A–U

Gigantodax cervicorne Wygodzinsky, 1973: 245. Vulcano, 1981: 276. Ramirez Perez, 1983: 72. [Incorrect gender]

DIAGNOSIS: Medium size species, with yellowish orange to light brown morphologically indistinctive imagos, but with peculiar pupal gill of five tubular branches with particular shape and disposition, and larva with a conspicuous gill histoblast.

REDESCRIPTION: *Female.* Length of wing 3.9–4.2 mm. Head dark gray, clypeus brown in some specimens; pilosity brass colored. Antenna, maxillary palp, and mouthparts dark brown; scapus, pedicellus, and base of first flagellomere orange colored, not strongly contrasting with flagellum. Scutum orange brown or very light reddish brown; scutellum yellowish, metanotum colored as in scutum; pleural regions of same general color as notum, darker on upper, lighter on lower, portion. Thoracic setae golden colored. Wing translucent; veins light brown on basal, dark brown on apical, half of wing. Hairs on stem vein dark colored, on remaining veins also dark. Halteres whitish, capitulum slightly tinged with brown. Legs from light orange to yellow, tarsal segments somewhat darkened; setae unicolorous. Abdominal tergites dark brown, tergites III and IV with conspicuous, and posterior tergites in some cases, testaceous mottling; hind border of tergites almost imperceptibly margined with whitish. Abdominal hairs brass colored.

Frontal angle 40–45°. Fronto-ocular triangle slightly higher than wide (fig. 148E). Shape and proportions of antennal segments as in figure 148H. Mandible with 26–29 teeth, outer margin slightly crenulated. Maxilla with about 25 teeth. Last segment of maxillary palp only slightly longer than penultimate (fig. 148I). Second segment of palp elongate oval, ratio length/width = 1:0.38–0.42. Sensory vesicle oval (fig. 148F). Sc with 24–26 hairs. R and R_1 with setae in one or rarely two irregular rows; R_1 also with numerous spinules beginning basal to level of insertion of Sc on C; spinules on apical portion of R_1 more numerous than setae (fig. 148L). R_s on distal portion on upper surface with a few setae and several spinules; undersurface of vein with setae arranged in two or three irregular rows. End of A_1 remote from wing margin. Shape and proportions of fore and hind leg segments as in figure 147A–C. Hind basitarsus 7.2–7.8 times as long as wide. Calcipala covering basal four-fifths of second tarsomere (fig. 148K). Basal tooth of claw comparatively small (fig. 148J). Abdominal sternites with only delicate

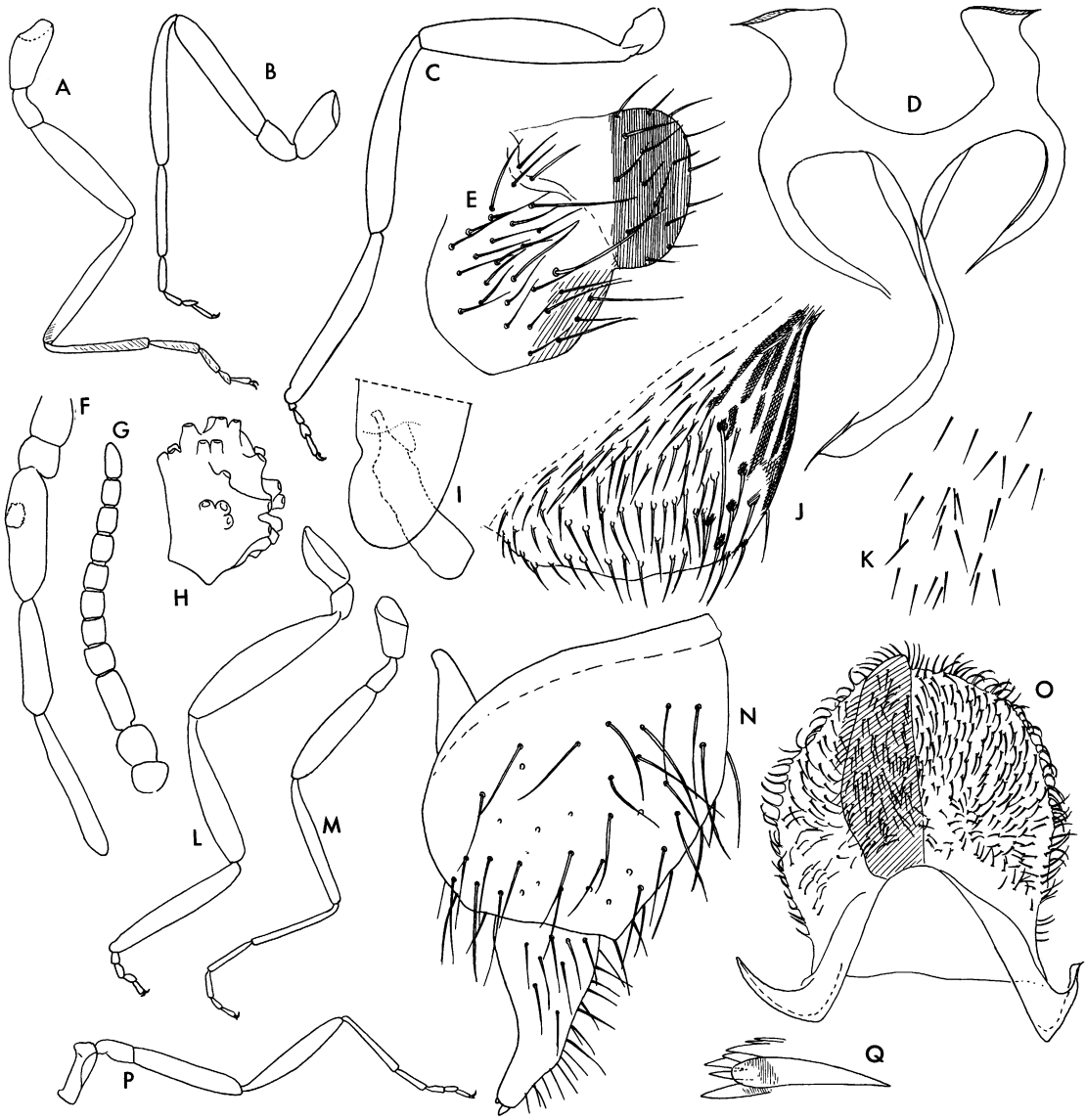

Fig. 147. *Gigantodax cervicornis.* A–E. Female. **A.** Foreleg. **B.** Mid leg. **C.** Hind leg. **D.** Genital fork. **E.** Cercus and paraproct. F–I. Male. **F.** Maxillary palp. **G.** Antenna. **H.** Sensory vesicle of maxillary palp. **I.** Calcipala, with second tarsal segment. **J.** Gonapophyses of female. **K.** Microstructure of spermatheca wall. L–Q. Male. **L.** Foreleg. **M.** Hind leg. **N.** Basimere and distimere. **O.** Ventral plate. **P.** Mid leg. **Q.** Endoparameral organ.

hairs. Gonapophyses, genital fork, and cercus with paraproct as shown in figure 147D, E, J; spermatheca with well-developed spicules (fig. 147K).

Male. Length of wing, 3.9–4.1 mm. Color much as in female but scutum bright yellowish orange. Holoptic. Shape and proportions of antennal segments as in figure 147G; ratio length/width of first flagellomere 1:0.44–0.51. Last segment of maxillary palp slightly longer than penultimate (fig. 147F). Sensory vesicle small, ovoid, with short neck (fig. 147H). Sc with 16–18 hairs; remainder of wing as in female, but spinules on upper surface of R_s

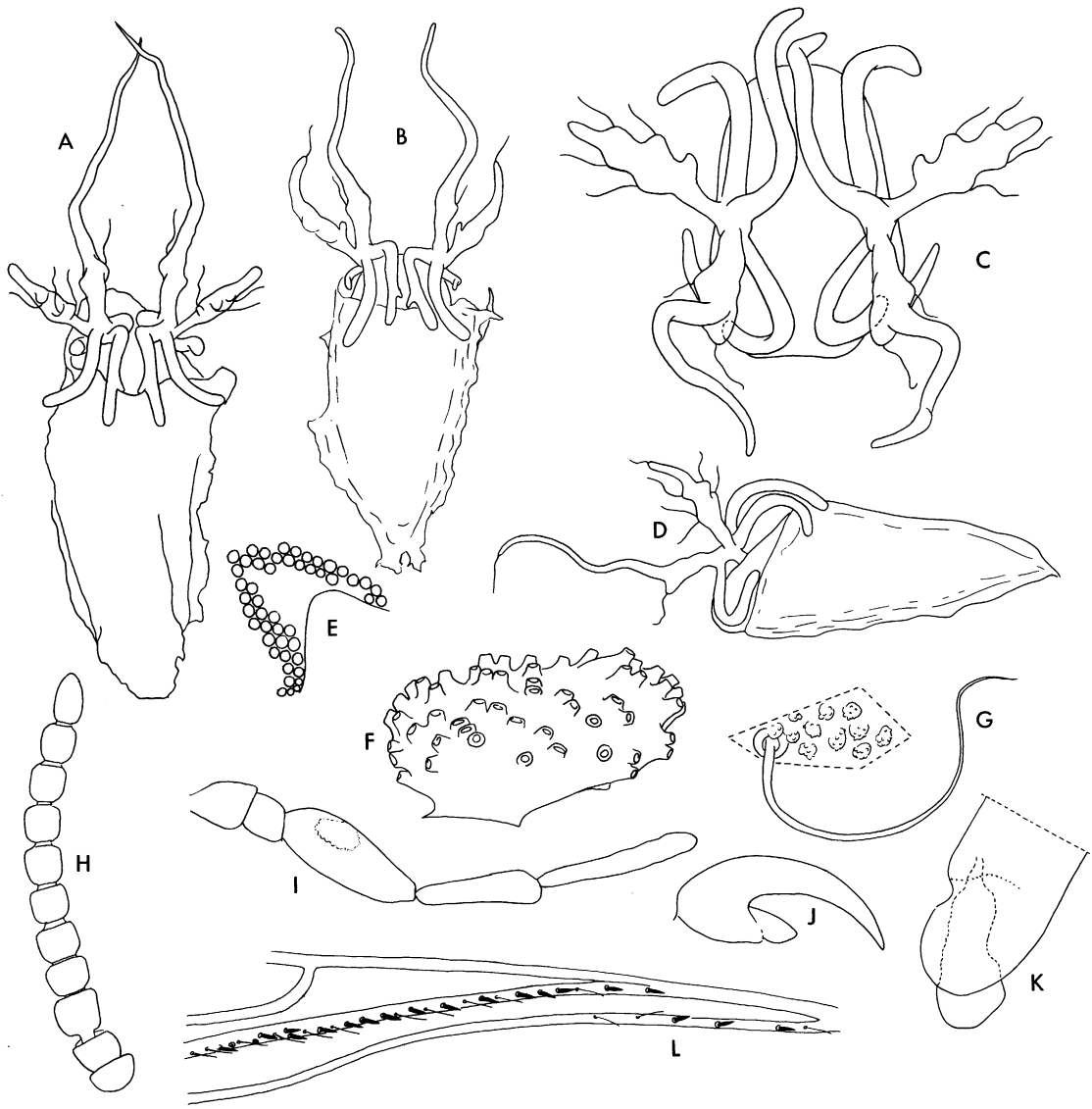

Fig. 148. *G. cervicornis.* **A, B.** Pupa in cocoon, dorsal view. **C.** Gill, frontal view. **D.** Pupa in cocoon, lateral view. E, F. Female. **E.** Fronto-ocular triangle. **F.** Sensory vesicle of maxillary palp. **G.** Thoracic trichome of pupa. H–L. Female. **H.** Antenna. **I.** Maxillary palp. **J.** Claw. **K.** Calcipala, with second tarsal segment. **L.** Portion of wing.

more slender than in female, or not developed. Shape and proportion of leg segments as in figure 147L, M, P; fore basitarsus 15.0–15.25 times, hind basitarsus 6.9–7.8 times, as long as wide. Calcipala (fig 147I) covering basal four-fifths of second tarsomere. Genitalia as shown in figure 147N, O, Q. Distimere approximately two-thirds as long as basimere, with two apical spines (fig. 147N). Main body of ventral plate as wide as long (fig. 147O). Hooks of endoparameral organ as in figure 147Q.

Pupa. Cocoon comparatively large, extending in most specimens to middle of thorax of pupa, anterior border not well defined (fig. 148A, B, D). Cocoon light brown, tightly woven, but translucent when not covered by foreign matter. Length of cocoon along dor-

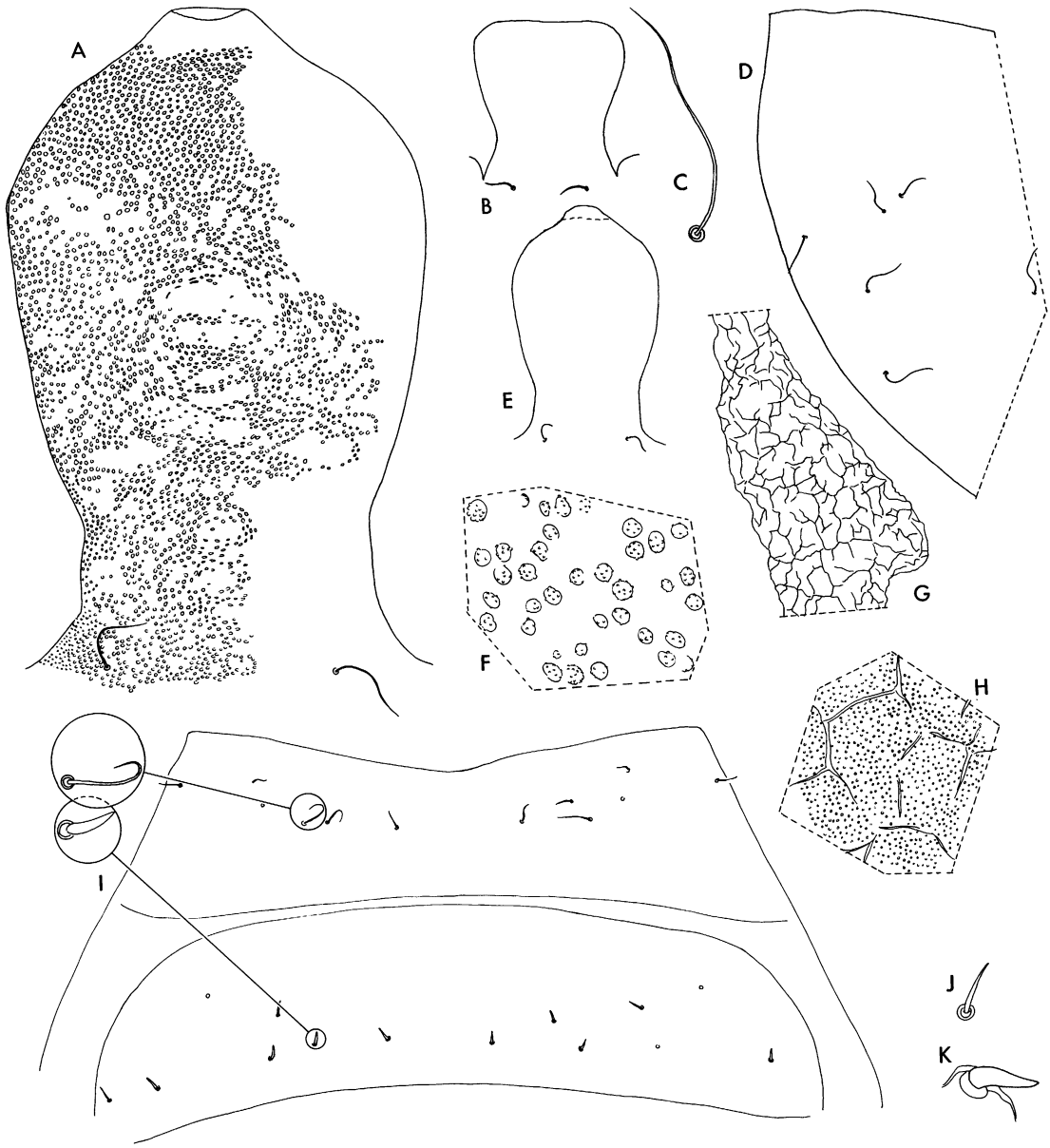

Fig. 149. G. *cervicornis*. Pupa. **A.** Frontoclypeus, male. **B.** Outlines of frontoclypeus, female. **C.** Trichome of thorax. **D.** Portion of thorax, with trichomes. **E.** Outline of frontoclypeus of male. **F.** Thoracic platelets. **G.** Surface of gill. **H.** Same, with high magnification. **I.** Chaetotaxy of abdominal tergites I and II. **J.** Anterosublateral spine of abdominal tergite III. **K.** Hook of abdominal tergite III.

sum 3–4 mm. Total length of pupal body about 4 mm, cephalopterothecal length 2.7 mm. Gills rigid, consisting each of five tubular branches: two dorsal, one sublateral, one anterior, and one ventral (fig. 148A–D). Inner dorsal branch short, backward curved over dorsum of thorax, cylindrical, rounded apically, at about center with rudimentary branch directed mesad. Outer dorsal arm cylindrical, simple, short, curved backward and outward. Sublateral arm directed laterad and somewhat upward, club-shaped, in some

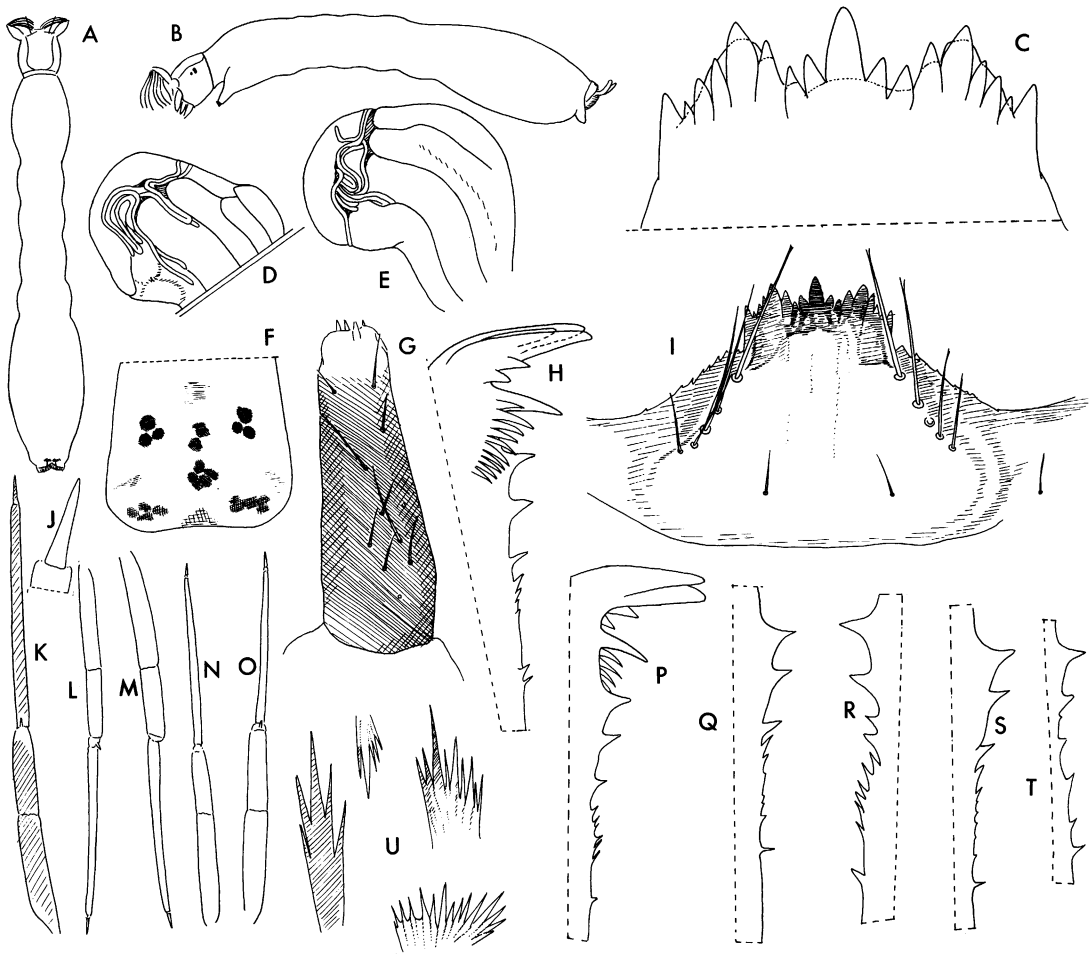

Fig. 150. *G. cervicornis.* Larva. **A.** Dorsal view. **B.** Lateral aspect. **C.** Teeth of hypostomium. **D, E.** Gill histoblasts. **F.** Cephalic apotome. **G.** Maxillary palp. **H.** Apex of mandible. **I.** Hypostomium. **J.** Apical sensillum of antenna. **K–O.** Antennae. **P.** Apex of mandible. **Q–T.** Mandibular serrations. **U.** Perianal scales.

specimens with distal portion drawn out, rounded apically; central swollen portion with five more or less prominent short protuberances, each bearing an apical respiratory filament, thus to be interpreted as strongly reduced branches. Anterior branch much longer than remaining, directed forward, narrowly drawn out anteriorly, subbasally swollen and with protuberances and short projection, some bearing an apical respiratory filament. Ventral branch simply cylindrical, U-shaped; basal portion downward, apical portion curved upward. Surface of gills rugose-reticulate (fig. 149G, H), color dark brownish gray; cuticular processes absent. Respiratory filaments caducous. Frontoclypeus of female and male as in figure 149B, E, with numerous heavily verrucose platelets distributed as in figure 149A. Facial trichomes long, hairlike (fig. 149C). Dorsocentral and dorsolateral trichomes of thorax hairlike (figs. 148G, 149D). Surface of thorax with approximately six rugose platelets (fig. 149F). Setae of abdominal tergite I hairlike, rather strong, length 50–80 μm; setae of tergite II spinelike, very short (30–35 μm) (fig. 149I). Tergites III and IV each with 4 + 4 short hooks (fig. 149K). Anterosublateral seta spinelike (fig. 149J). Setae of tergites V–VIII slender, length on tergite VII 55–60 μm. Spine-combs on tergites VI–

VIII variously interrupted, consisting on tergite VII of 27–33 spines, length 20–30 μm, viz., about one-third of length of this setae of this tergite. Specialized setae of segments VIII and IX simple or bifid. Sternite IV with small hooklike setae, in some specimens in three groups of two setae each. Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 7.8–8.5 mm; width of head capsule about 0.8 mm. Body shape normal for the genus (fig. 150A); ventral papillae distinct (fig. 150B). Color of larva whitish, with extensive dark hypodermal pigment, most intense on posterior portion of body. Head capsule light brown; spots of cephalic apotome distinct (fig. 150F). Hypostomial bridge lightly darkened, with median longitudinal line whitish. Antenna as long as stem of cephalic fan, distinctly pigmented, third segment darkest. Shape of antenna as in figure 150K-O; ratio of segments I–III = 1:0.60–0.74:1.24–1.57. Terminal sensillum about 4.5 times as long as wide at base (fig. 150J). Cephalic fan with 28–32 large rays. Mandible (fig. 150H, P–T) with 8–11 inner teeth and 7–10 marginal serrations. Maxillary palp slightly less than three times as long as wide (fig. 150G). Hypostomium as in figure 150I, C. Median tooth slightly beyond level of corner tooth apex; line connecting apex of median tooth to apex of fourth lateral tooth intersecting several other teeth; line connecting apices of fourth lateral and corner teeth meeting at right angle. Hypostomium with 6–9 lateral serrations and 4–6 hypostomial setae in each row. Cervical sclerites as in *G. cormonsi.* Gill histoblast black, its structure as illustrated (fig. 150D–E), only a single transverse portion of branch on apical region; respiratory filaments conspicuous. Perianal scales large, conspicuous, strongly pigmented (fig. 150U), forming complete circumanal ring. Recurrent struts well developed. Crochet ring with 100–120 rows of 20–22 hooks each.

MATERIAL EXAMINED: ECUADOR: *Pichincha:* 1 km W of Laguna de Papallacta, 3300 m, Aug. 4, 1969 (P. and B. Wygodzinsky; AMNH), 2 females (reared, and with associated pupal exuviae), 1 larva; road from Aloag to Santo Domingo de los Colorados, 2200 m, Aug. 9, 1969 (P. and B. Wygodzinsky; AMNH), 1 larva. COLOMBIA: *Cauca:* road from Popayan to Paramo de Purace, 3300 m, Aug. 17, 1967 (P. and B. Wygodzinsky; AMNH), 1 pupa. *Quindio:* road from Ibague to Calarca, 3000 m, Aug. 14, 1967 (P. and B. Wygodzinsky; AMNH), larvae. *Cundinamarca:* 2 km SE of Alban, 2400 m, Aug. 6, 1967, Aug. 24, 1969 (P. and B. Wygodzinsky; AMNH), 1 male, holotype, 1 female, allotype, 18 males and 33 females, paratypes (reared, and with associated pupal exuviae), pupae and larvae; on road from Sibate to Aguadita, 2270 m, July 5 and 25, 1967 (P. and B. Wygodzinsky; AMNH), 16 males, 8 females (reared, and with associated pupal exuviae), pupae, and larvae; ibid., 2300 m, July 5, 1967 (P. and B. Wygodzinsky; AMNH), pupae; E of La Siberia, 3150 m, Aug. 26, 1969 (P. and B. Wygodzinsky; AMNH), pupae, 1 larva; Paramo de Guasca, 2850 m, July 20, 1967 (P. and B. Wygodzinsky; AMNH), larvae; 3 km S of Chipaque, 2400 m, July 30, 1967 (P. and B. Wygodzinsky; AMNH), 1 female (reared, and with associated pupal exuviae). VENEZUELA: *Merida:* SW of Mucuruba, 2350 m, Feb. 9–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 3 males, 1 female (reared, and with associated pupal exuviae), pupae; N of Apartaderos, 3850 m, Feb. 13, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), pupae; Apartaderos, 3550 m, Feb. 9, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), pupae; road from Apartaderos to Santo Domingo, 3400 m, Feb. 16–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), pupae; ibid., 3050 m, Feb. 16–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 male, 5 females (reared, and with associated pupal exuviae), pupae.

BIOLOGY: The aquatic instars of this species have been found in small streams from 1 to 5 ft wide, in areas of montane cloud forest to paramo. The water temperature ranged from 9 to 17°C, most commonly 14 to 16°C. Pupae were adhering to the sides, and more frequently, to the undersurfaces of large stones in the stream bed, the insects apparently preferring small cracks and dells. In many cases, pupae were also found attached to the underside of watercress leaves or to the upper

surface of grass blades trailing in the stream, the pupae being generally situated along the mid rib of the blade.

DISCUSSION: The pupal gills are sufficient to distinguish this species from all others of the genus. The gill structure is of the same basic pattern as that of *G. corniculatus*; the differences between the two species are detailed under the diagnosis of the latter. *G. cervicornis* seems to have a much wider range, extending from Venezuela to Ecuador; *corniculatus* has so far only been collected in Venezuela where its range overlaps that of *cervicornis*.

Gigantodax corniculatus Wygodzinsky
Figures 151A–S, 152A–J, 153A–L, 178F

Gigantodax corniculatum Wygodzinsky, 1973: 243. Vulcano, 1981: 276. Ramirez Perez, 1983: 73. [Incorrect gender]

DIAGNOSIS: Medium size species with imagos reddish yellow-brown, calcipala about three-fourths as long as second tarsomere, pupa with gill branches conspicuously wrinkled and without cuticular processes, with five main tubular branches and some very short ones; larva with antenna as long as mouthfan stem and median tooth as long as corner tooth.

REDESCRIPTION: *Female.* Length of wing 4.6–4.8 mm. Color of head and appendages as in *cervicornis*. Scutum dull reddish brown; scutellum yellowish brown, metanotum dark pruinose. Pleura from yellowish to reddish brown. Thoracic setae golden yellow. Color of wing, halter, legs, and abdomen as in *cervicornis*.

Frontal angle 50°. Fronto-ocular triangle about as high as wide. Shape and proportions of antennal segments as in figure 151L. Mandible with approximately 24 teeth; outer margin faintly crenulated apically. Maxilla with about 26 teeth. Distal segment of maxillary palp very slightly longer than penultimate (fig. 151C). Second segment of palp elongate oval, ratio length/width = 1:0.47–0.48. Sensory vesicle elongate suboval, without distinct neck (fig. 151A). Sc with 24–29 hairs. R with setae in two or three irregular rows. R_1 with setae in one row, interspersed with spinules, the latter beginning distinctly basal to level of insertion of Sc on C; apical portion of R_1 with spinules more numerous than setae, arranged in one or two rows. R_s on distal portion of upper surface with one row of setae, several of which are somewhat similar to spinules; undersurface of R_s with setae in several rows. A_1 not reaching to wing margin. Shape and proportions of fore and hind leg segments as in figure 151E, J. Hind basitarsus 7.5–7.7 times as long as wide. Calcipala well beyond middle of second tarsomere, covering approximately four-fifths its length (fig. 151H). Basal tooth of claw as in figures 151D, 178F. Abdominal sternites with only delicate hairs. Eighth sternite and gonapophyses without special characters; cercus with paraproct and genital fork as illustrated (fig. 151I).

Male. Length of wing 4.1–4.2 mm. Color much as in female, but scutum bright reddish orange. Holoptic. Shape and proportions of antennal segments as in figure 151K; ratio length/width of first flagellomere 1:0.53–0.56. Distal segment of maxillary palp slightly longer than penultimate (fig. 151G). Sensory vesicle small, ovoid, with distinct neck (fig. 151O, P). Sc with 14–16 setae; all setae of upper surface of R_s simple; wing otherwise as in female. Shape and proportion of fore and hind leg segments as in figure 151Q, R. Fore basitarsus 14–15 times, hind basitarsus about 6.5–7.0 times, as long as wide. Calcipala (fig. 151N) covering two-thirds of second tarsomere. Genitalia as in *cervicornis*. Basimere, distimere, and ventral plate as in figure 151M, S.

Pupa. Cocoon extending dorsally to base or at most to center of thorax, anterior border irregularly shaped (fig. 152B, G). Cocoon light brown tightly woven, translucent. Length of cocoon along dorsum 3.8–4.1 mm, somewhat longer ventrally. Total length of pupal body 4.2–5.0 mm; cephalopterothecal length 3.8 mm. Gill rigid, with five main tubular branches: two dorsal, one sublateral, one anterior, and one ventral (fig. 152A, B, G, H). Inner dorsal and outer dorsal branches as in *cervicornis*. Sublateral branch directed laterad and somewhat forward and upward, shortly beyond its base divided into cluster of five short and two long arms, longer arms conspicuously narrowed toward apex. Anterior branch with one short and two subequal arms, long ones directed forward, the latter pointed

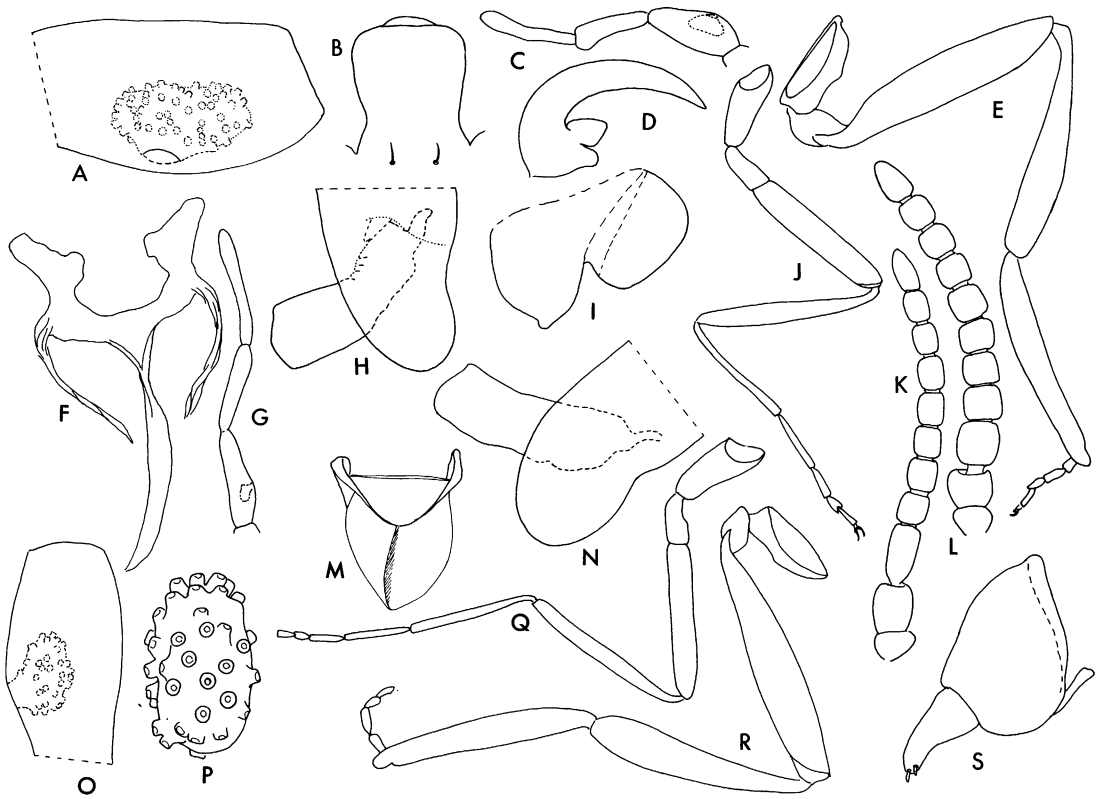

Fig. 151. *Gigantodax corniculatus.* A–F. Female. **A.** Second article of maxillary palp. **B.** Outline of female frontoclypeus. **C.** Maxillary palp. **D.** Claw. **E.** Posterior leg. **F.** Genital fork. **G.** Maxillary palp of male. H–J. Female. **H.** Calcipala, with second tarsal article. **I.** Cercus and paraproct. **J.** Foreleg of female. **K.** Antenna of male. **L.** Antenna of female. M–S. Male. **M.** Ventral plate. **N.** Calcipala, with second tarsal article. **O.** Second segment of maxillary palp. **P.** Sensory vesicle of second segment of maxillary palp. **Q.** Foreleg. **R.** Posterior leg. **S.** Basimere and distimere.

apically. Ventral branch as in *cervicornis.* Arms of lateral and anterior branches each apically with caducous respiratory filaments. Surface structure and color of gills as in *cervicornis.* Frontoclypeus of male with very numerous almost uniformly distributed verrucose platelets (fig. 151F). Facial trichomes spinelike. Thorax with platelets verrucose, irregularly distributed. Dorsocentral (fig. 152C) and dorsolateral trichomes in shape of very delicate hairs, numbering five or six. Abdominal onchotaxy as in *cervicornis.* Hooks of abdominal tergites II and III as in figure 152E, I, respectively; seta of abdominal tergite III as in figure 152J.

Mature larva. Length 7.8–8.5 mm; width of head capsule about 0.8 mm. Body shape normal for the genus (fig. 153B); ventral papillae distinct. Color of larva whitish, with faint overall hypodermal pigment, darkest on posterior portion of body. Color and pattern of head capsule as in *cervicornis.* Antenna as long as stem of cephalic fan, very weakly pigmented, third segment not darker than preceding. Shape of antenna as in figure 153C, H; ratio of segments I–III = 1:0.66–0.81:1.35–1.51. Terminal sensillum about 4.6 times as long as wide at base (fig. 153A). Mandible (fig. 153D–G, I) with 8–10 inner teeth and 4–9 marginal serrations. Maxillary palp about 2.6 times as long as wide. Hypostomium as in figure 153K. Median tooth reaching to but not beyond level of corner tooth apex. Line connecting apex of median tooth to apex of fourth lateral tooth intersecting several other teeth; lines connecting apex of fourth lateral

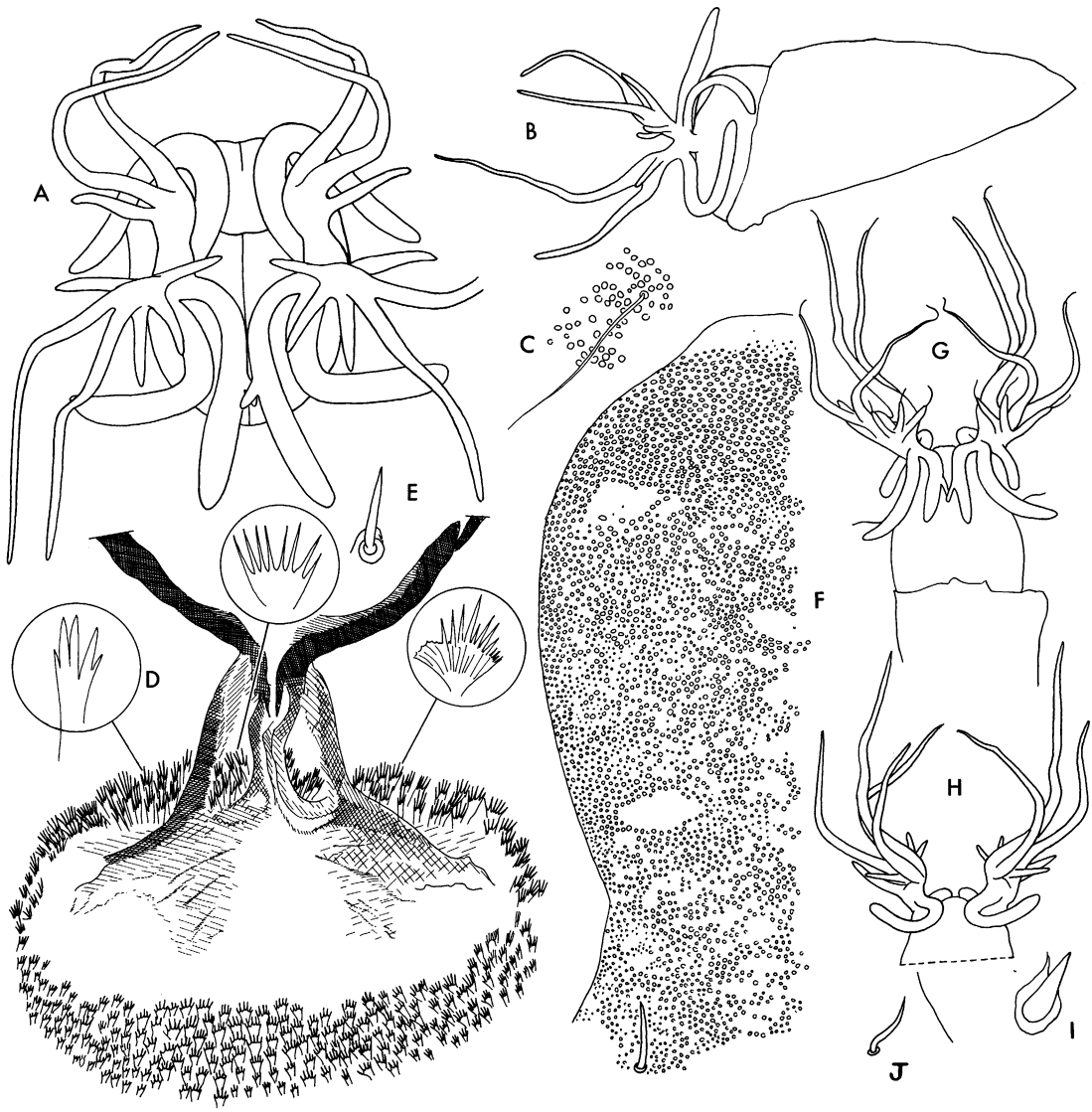

Fig. 152. *G. corniculatus.* **A.** Head and gills of pupa, frontal view. **B.** Pupa in cocoon, side view. **C.** Dorsocentral trichome of thorax. **D.** Anal sclerite of larva. **E.** Hook of abdominal tergite II. **F.** Frontoclypeus of male with platelets. **G.** Anterior portion of pupa, dorsal aspect. **H.** Same, ventral view. **I.** Hook of abdominal tergite III. **J.** Seta of abdominal tergite III.

tooth to apex of corner tooth meeting at angle of 110–120°. Cephalic fan with 28–32 large rays. Teeth of cephalic fan as in figure 153L. Hypostomium with seven to nine lateral serrations and four to six hypostomial setae in each row. Cervical sclerites as in *G. cormonsi.* Gill histoblast black, structure as shown in figure 153J, with several transverse portions of branches on apical region of histoblast; respiratory filaments visible. Perianal scales extremely well developed (fig. 152D), forming conspicuous circumanal ring. Recurrent struts well developed. Crochet ring with 80–94 rows of 20–23 hooks each.

HOLOTYPE: VENEZUELA: *Merida:* on road from Apartaderos to Santo Domingo, 3400 m, Feb. 16–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: VENEZUELA: *Merida:* SW of Mucuruba, 2350 m, Feb. 9–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 larva; same data as holotype, 1 female, allotype, 8 males, 11 females, paratypes (all reared, and with associated pupal exuviae), pupae, and larvae; ibid., 3050 m, Feb. 16–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), pupae; Apartaderos, 3550 m, Feb. 9, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 male (reared, and with associated pupal exuviae), pupae, and larvae; N of Apartaderos, 3700 m, 3850 m, 4000 m, Feb. 13, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 3 females (reared, and with associated pupal exuviae), pupae, and larvae; outlet of Laguna Mucubaji, 3600 m, Feb. 16, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 pupa, 1 larva.

BIOLOGY: This species was found in small and medium size fast flowing mountain streams from 15 cm to 3 m wide, located above 3000 m, in the paramo formation. Water temperatures were between 10 and 16°C. Pupae were invariably attached to the undersurfaces of large stones. At most collection sites *corniculatus* occurred together with *G. cervicornis,* although at the highest collecting point for *corniculatus, cervicornis* was not found, and at the lowest site for *cervicornis* (2350 m) *corniculatus* was very rare.

DISCUSSION: This species is in many respects very similar to *G. cervicornis,* according to the overall structure of the pupal gill and the frequent presence of spinulets, or spinuletlike setae, on R_s. The main differences are the following: *G. corniculatus* is somewhat larger, especially the adult. The scutum of the female of *cervicornis* is orange brown or very light reddish brown, and in the male bright yellowish orange; in *corniculatus,* the scutum of the female is dull reddish brown, and reddish orange in the male. The sensory vesicle of the maxillary palp is smaller in *cervicornis* than in *corniculatus.* The differences in the gills of the pupa are mainly in the length of the arms of the sublateral and anterior branches, many of which are reduced to faint protuberances in *cervicornis,* where their location can be established only through the point of insertion of the respiratory filaments. The pupal facial trichomes of *corniculatus* are spinelike, those of *cervicornis* hairlike. The mature larvae can be distinguished with certainty only by the gill histoblast.

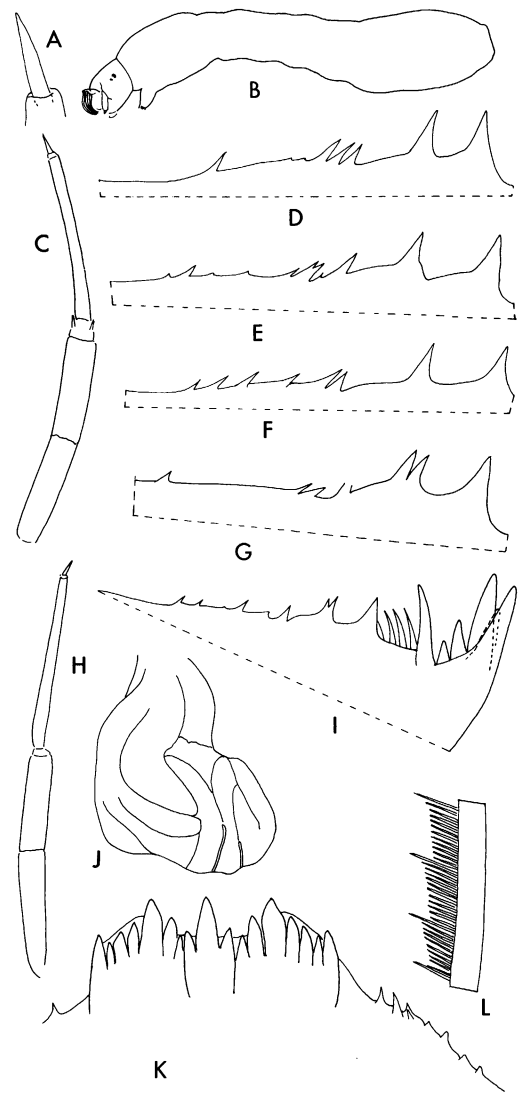

Fig. 153. *G. corniculatus.* Larva. **A.** Sensillum of apex of antenna. **B.** Larva, side view. **C.** Antenna. **D–G.** Lateral serrations of mandible. **H.** Antenna. **I.** Apex of mandible. **J.** Gill histoblast. **K.** Distal portion of hypostomium. **L.** Teeth of ray of cephalic fan.

Gigantodax wrighti
(Vargas, Martinez and Diaz)
Figures 154A–Z, AA–CC, 155A–I, 156A–M

Simulium (*Gigantodax*) *wrighti* Vargas, Martinez, and Diaz, 1944: 37.

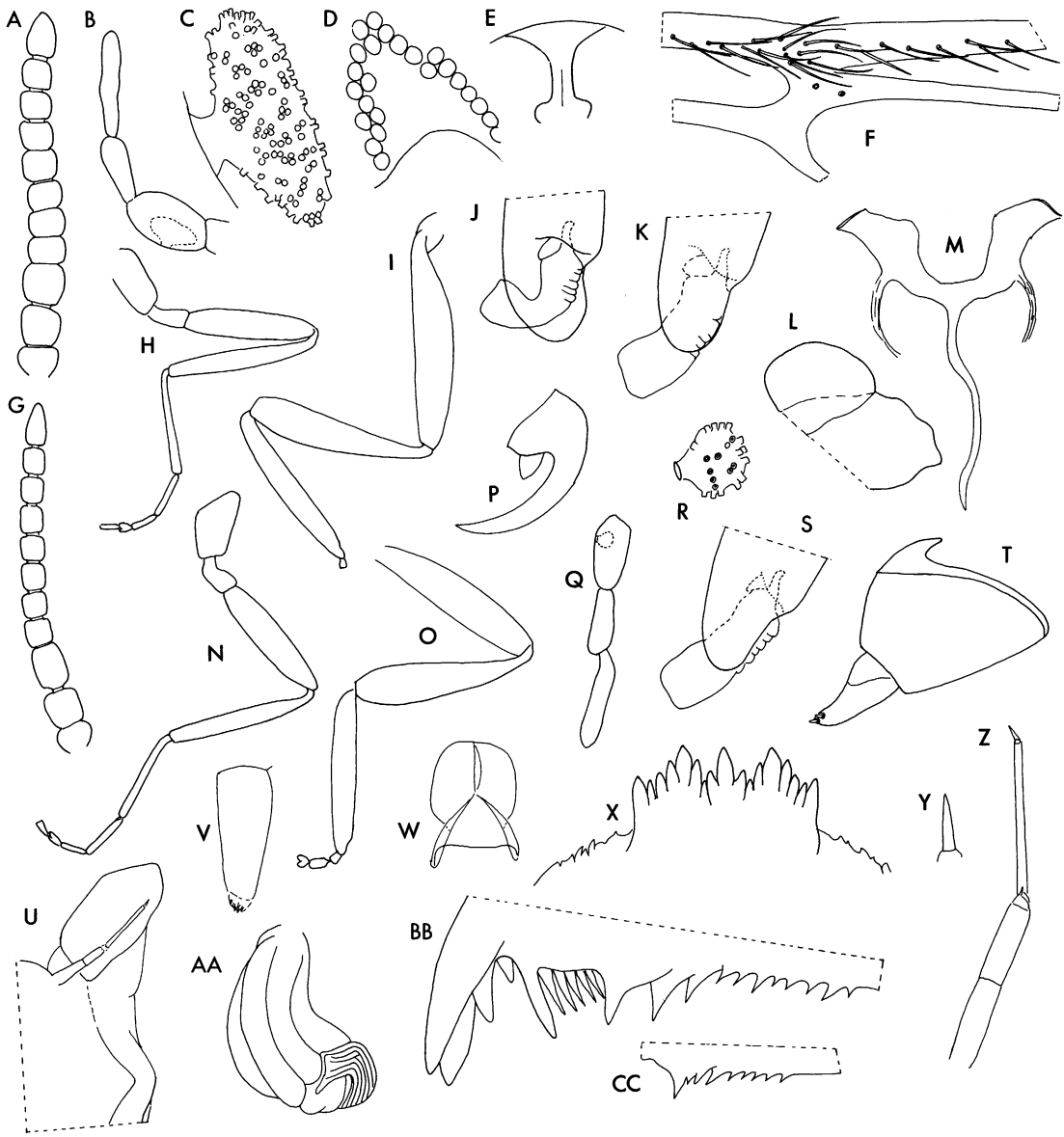

Fig. 154. *Gigantodax wrighti.* A–F. Female. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle of maxillary palp. **D.** Fronto-ocular triangle. **E.** Frons and vertex. **F.** Portion of wing, area of r-m cross-vein. **G.** Antenna of male. H–M. Female. **H.** Foreleg. **I.** Hind leg. **J, K.** Calcipala and second tarsal segment. **L.** Cercus and paraproct. **M.** Genital fork. **N.** Foreleg of male. **O.** Hind leg of male. **P.** Claw of female. Q–T. Male. **Q.** Maxillary palp. **R.** Sensory vesicle of maxillary palp. **S.** Calcipala and second tarsal segment. **T.** Basimere and distimere. **U.** Portion of head of larva, with antenna and stem of mouth fan. **V.** Maxillary palp of larva. **W.** Basal plate of genitalia of male. X–CC. Larva. **X.** Anterior portion of hypostomium. **Y.** Terminal sensillum of antenna. **Z.** Antenna. **AA.** Gill histoblast. **BB.** Apical portion of mandible. **CC.** Mandibular serrations.

Simulium wrighti: Vargas, 1945: 213.
Gigantodax wrighti: Vargas, Martinez, and Diaz, 1946: 165. d'Andretta, 1947: 24. Dalmat, 1955: 107. Vargas and Diaz, 1957: 156. Vulcano, 1967: 4. Okazawa and Nodasaka, 1982: 95.

Simulium (*Gigantodax*) *vargasi* de Leon, 1945: 69. [synonym]

DIAGNOSIS: Medium-size, brownish imagos having calcipala two-thirds the length of

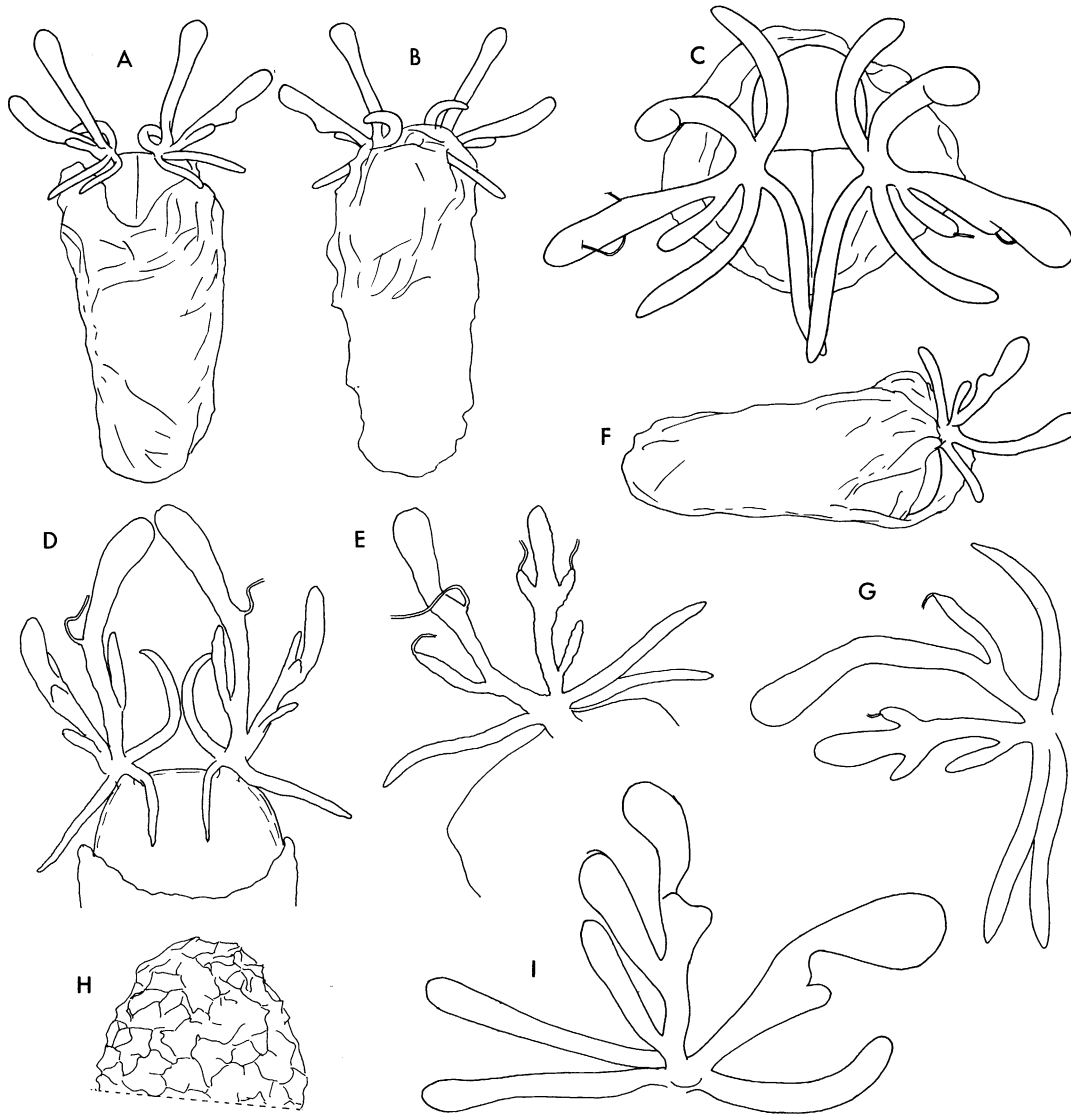

Fig. 155. *G. wrighti.* Pupa. **A.** Pupa in cocoon, dorsal view. **B.** Same, ventral aspect. **C.** Anterior portion of body with gills, frontal view. **D.** Same, dorsal aspect. **E.** Gill. **F.** Pupa in cocoon, lateral view. **G.** Gill. **H.** Cuticular structure of apex of gill branch. **I.** Gill.

second tarsomere; pupal gill with 6–9 tubular branches, the anterior branch swollen distally; median tooth at same level as corner tooth and larval gill histoblast with tubular and filamentous branches.

REDESCRIPTION: *Female.* Length of wing 4.1–4.3 mm. Head dark gray, clypeus brownish, pilosity brass colored. Antenna and maxillary palp dark brown; scapus, pedicellus, and base of first flagellomere orange, remaining flagellomeres tinged with orange. Scutum, scutellum, and metanotum dull reddish brown. Pleural region of same general color, somewhat lighter anteriorly and on lower portion. Thoracic setae brass colored. Wing translucent; setae of stem vein and all other veins dark. Halter whitish, slightly tinged with brown, especially on capitulum. Legs light brown; setae concolorous. Abdominal tergites piceous, somewhat lighter on center of disc, posterior margin very narrowly lighter. Abdominal hairs brass colored.

Frontal angle 60°. Front with small sulcus (fig. 154E). Fronto-ocular triangle about as

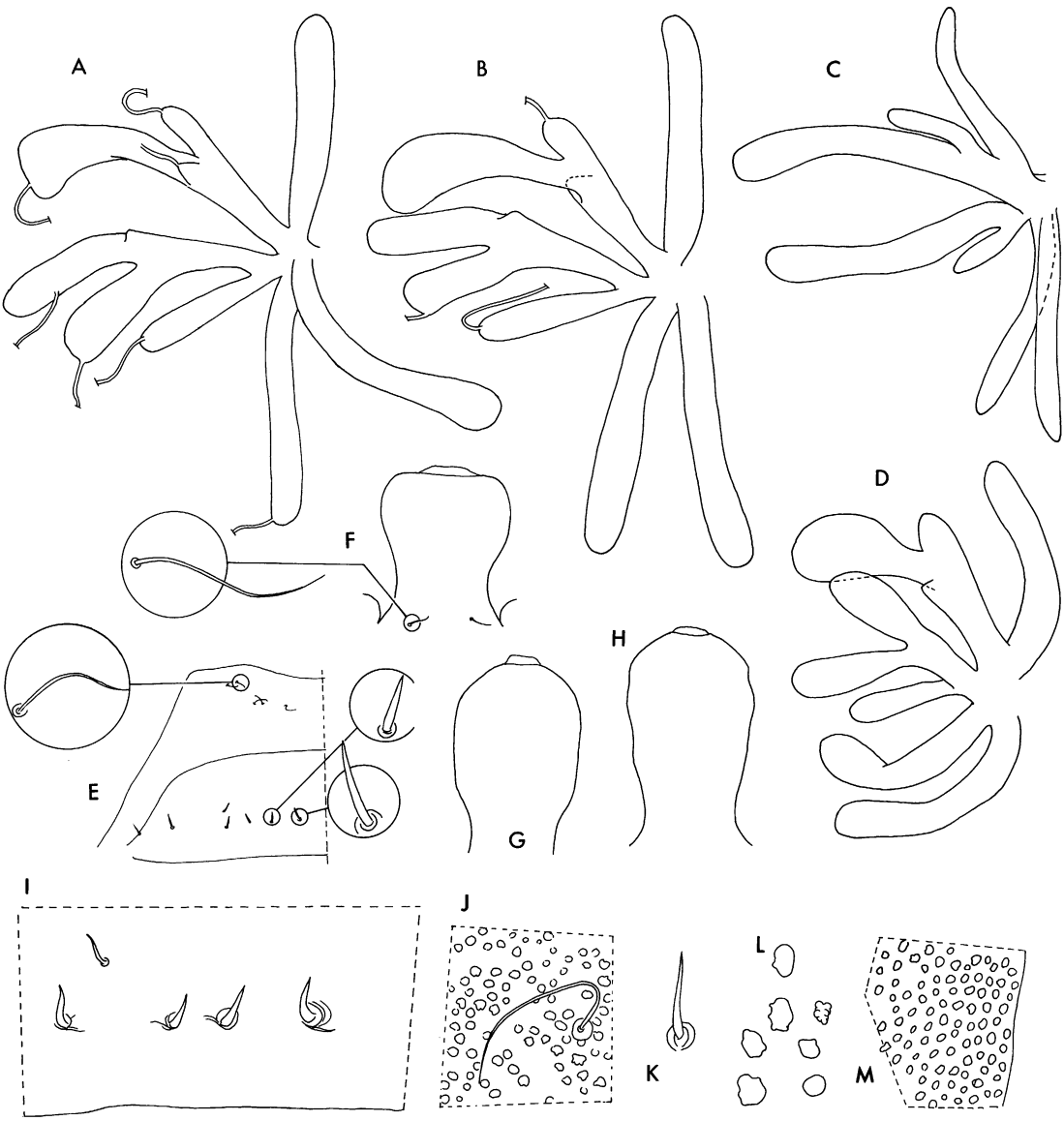

Fig. 156. *G. wrighti.* Pupa. **A–D.** Gills. **E.** Chaetotaxy of abdominal tergites I and II. **F.** Outline of frontoclypeus of female. **G.** Outline of frontoclypeus of male. **H.** Same, different specimen. **I.** Hooks of tergite IV. **J.** Detail of thorax, with platelets and trichome. **K.** Spinelike seta of abdominal tergite II. **L.** Platelets of thorax. **M.** Platelets of clypeus.

high as wide (fig. 154D). Shape and proportions of antennal segments as in figure 154A. Mandible with 18–21 teeth only on inner margin. Maxilla with 16–19 teeth. Last segment of maxillary palp less than twice as long as penultimate (fig. 154B). Second segment shortly suboval, ratio length/width = 1:0.57–0.67. Sensory vesicle (fig. 154C) very large, with short neck. Sc with 18–20 hairs. R with setae in a single row, double only at extreme base of vein. Setae clustered at junction of R and R_1. R_1 (fig. 154F) with one or two rows of setae, spinules present but not numerous, beginning apical to level of insertion of Sc on C. R_s with setae in one row on apical portion of upper surface of vein, in two to three rows

on undersurface. A_1 not reaching wing margin. Shape and proportions of fore and hind legs as in figure 154H–I. Hind basitarsus 6.9 times as long as wide. Calcipala extended slightly beyond center of second tarsomere (fig. 154J). Basal tooth of claw very small (fig. 154P). Abdominal sterna with only delicate hairs. Genitalia without special characters; cercus, paraproct, and genital fork as shown in figure 154L, M.

Male. Wing length 3.5–3.7 mm. General color as in female, but scutum deep reddish brown, and abdominal tergites not lightened on disc.

Holoptic. Shape and proportions of antennal segments as in figure 154G; ratio length/width of first flagellomere 1:0.67–0.77. Last segment of maxillary palp less than twice as long as penultimate (fig. 154Q). Sensory vesicle (fig. 154R) small, subglobular, with distinct neck. Wing much as in female; Sc with 14 setae. Shape and proportions of fore and hind leg segments as in figure 154N, O. Fore basitarsus 11.3 times, hind basitarsus 6.13–6.63 times as long as wide. Calcipala extended slightly beyond middle of second tarsomere (fig. 154S). Distimere about two-thirds as long as basimere, with two apical spines (fig. 154T). Main body of ventral plate about as long as wide, characterized by almost straight lateral margins (fig. 154W).

Pupa. Cocoon baglike, completely covering body of pupa except gills (fig. 155A, B, F). Color of cocoon dark brown; formed by coarse, irregular mesh, invariably incrusted with small organic and inorganic particles. Length of cocoon 3.5–4.0 mm. Total length of pupal body 3.8–4.6 mm; cephalopterothecal length 2.5 mm. Gill rigid, with six to nine tubular branches, some reduced in certain specimens to mere protuberances (figs. 155A–G, I, 156A–D). Gill with five primary branches: two dorsal, one sublateral, one anterior, and one ventral. Dorsal branches simple, subvertical, rounded but not with apex perceptibly widened apically. Sublateral branch with subbassal arm, trifid further apicad, bifid or even simple, main branch strongly swollen apically, the others variously developed, from complete branches to almost imperceptible protuberances. Anterior branch directed forward, club shaped, corresponding to branches. Surface of branches reticulated (fig. 155H). Apically with caducous respiratory filament (fig. 155A–E). Shape and proportions of frontoclypeus of both sexes as shown in figure 156F–H, with numerous regularly spaced, lightly verrucose platelets. Facial trichomes in form of strong hairs. Thorax with numerous, rather regularly spaced, slightly verrucose platelets (fig. 156L). Dorsocentral and dorsolateral trichomes hairlike (fig. 156J). Setae of abdominal tergite I in shape of strong hairs (fig. 156E), their length 50–70 μm. Setae of tergite II spinelike, their length 35–50 μm. Tergites II and IV each with 4 + 4 short hooks (fig. 156I); anterosublateral seta in shape of small hook (fig. 156K). Setae of tergites V–VIII slender, those on VI and VII inconspicuous, length 35–40 μm. Spinecombs on segments VI–VIII, continuous, consisting on tergite VII of 35–38 spines, length 20–25 μm, viz., over half as long as setae of this segment. Specialized setae of segments VIII and I variously bent but not branched. Sternite IV with short hooklike setae arranged in three groups of two. Sternite V with 3 + 3, VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 7.0–7.5 mm; width of head capsule 6.5–7.5 mm. General shape as typical for genus; ventral papillae small but distinct. General color of larva whitish, with hypodermal pigment from almost imperceptible to faint (most specimens) and to very intensive. Head color very variable, from light yellowish white with pattern of cephalic apotome distinct, to brown with pattern blending into ground color. In all specimens, hypostomial bridge very slightly darker compared to lateral areas of undersurface of head, with faintly perceptible median longitudinal, light-colored stripe. Antenna slightly shorter than stem of cephalic fan (fig. 154U), somewhat pigmented, third segment darker than two preceding. Shape of antenna as in figure 154Z; ratio of segment I–III = 1:0.70–0.92:1.46–1.60; first and second segments combined less than seven times as long as width of second segment . Terminal sensillum 4.8 times as long as wide at base (fig. 154Y). Cephalic fan with 22–26 large rays. Mandible (fig. 154BB) with 8–10 inner teeth and 9–11 marginal serrations. Maxillary palp about 2.5

times as long as wide at base (fig. 154V). Hypostomial teeth as in figure 154X. Median tooth reaching to but not beyond, level of corner tooth apex. Line connecting fourth lateral tooth and corner tooth apices meeting at angle of 110–120°; 4–5 hypostomial setae and 6–7 lateral serrations. Cervical sclerites as in *G. cormonsi.* Gill histoblast as in figure 154AA, with four main branches. Perianal scales well developed, forming distinct perianal ring. Anal sclerite with well developed recurrent struts. Crochet ring with 84–93 rows of 20–27 hooks.

MATERIAL EXAMINED: MEXICO: *Distrito Federal:* El Zarco, 3100 m, Sept. 9–17, 1969 (P. and B. Wygodzinsky; AMNH), 3 males (reared, and with their associated pupal exuviae), pupae, and larvae. *Mexico:* road to Tlamacaz, W slope of Mt. Popocatepetl, 3400 and 3500 m, Sept. 15, 1969 (A. Barrer, E. Martin, P. and B. Wygodzinsky; AMNH), 1 male, 1 female (reared, and with their associated pupal exuviae), pupae, and larvae. We have also examined material from El Porvenir, Chiapas, Mexico, and from Acatenango, Guatemala.

DISTRIBUTION: *Gigantodax wrighti,* the northernmost species of the genus, is now known in Mexico from the Federal District and the state of Mexico, Veracruz, Oaxaca, and Chiapas, and from various highland departments of Guatemala. The species, as already shown by Dalmat (1955), is almost entirely restricted to altitudes above 2000 m, and attaining, at least in Mexico, an altitude of 3500 m.

DISCUSSION: The closest species is *aquamarensis* and the differences are explained in the discussion of that species.

Gigantodax nasutus, new species
Figures 157A–S, 158A–M

DIAGNOSIS: The extremely elongate mouthparts of the female and the five tubular branches of the pupal gills are sufficient to characterize the species.

DESCRIPTION: *Female.* Wing length 4.0 mm. Head lead gray, clypeus tinged with orange. Antenna and maxillary palp dark brown; scapus, pedicellus, and base of first flagellomere orange colored. Mouthparts dark brown. Head hairs brass colored. Scutum very light reddish brown, almost orange. Scutellum light yellow. Metanotum reddish brown. Setae of thorax golden colored. Pleuron pale orange. Wing translucent; areas between Sc and R yellow; veins dark brown. Setae on stem vein and on other veins dark. Halteres whitish, faintly tinged with brown. Legs very pale orange or yellow, apices of femora and tibiae very slightly darkened. Abdominal terga piceous, with hind margin narrowly bordered with ivory white, disc of terga faintly mottled with ivory white. Abdominal hairs golden yellow.

Frontal angle 65°. Fronto-ocular triangle about as high as wide (fig. 157B). Shape and proportions of antennal segments as in figure 157K. Mouthparts extraordinarily elongate (fig. 157A, C, F), somewhat longer than face and height of head. Labrum four times longer than wide at base. Mandible eight times as long as maximum width (fig. 157I), with about 55 normally developed teeth (fig. 157D). Distal segment of maxillary palp as long as penultimate (fig. 157E, G). Second segment of palp extraordinarily slender and elongate (fig. 157H), ratio length/width = 1:0.24. Sensory vesicle as in figure 157O, with extremely short neck; Sc with 21 hairs. Proboscis elongate, as in figure 157F. R and R_1 with setae arranged in one somewhat irregular row, interspersed on R_1 with spinules, latter beginning distinctly proximal to level of insertion of Sc on C. R_s above with setae in one row, below in one or two irregular rows. A_1 almost reaching to wing margin. Shape and proportions of leg segments as in figure 157J, L. Hind basitarsus 7.3 times as long as wide. Calcipala almost reaching to apex of second tarsomere (fig. 157N). Basal tooth of claw as in figure 157R. Abdominal sterna membranous throughout, sterna with only delicate hairs. Eighth sternite with 17 + 17 setae. Gonapophyses with microtrichia and a few short hairs. Spermatheca (fig. 157S) sclerotized until bare at neck. Genital fork, cerci, and paraprocts as in figure 157M, Q.

Male. Unknown.

Pupa. Cocoon covering pupa to base of thorax (fig. 158A, B, F), its color light brown, translucent, tightly woven but individual threads perceptible. Length of cocoon along dorsum 4.0 mm. Total length of body of pupa 5.0 mm; cephalopterothecal length 2.8 mm.

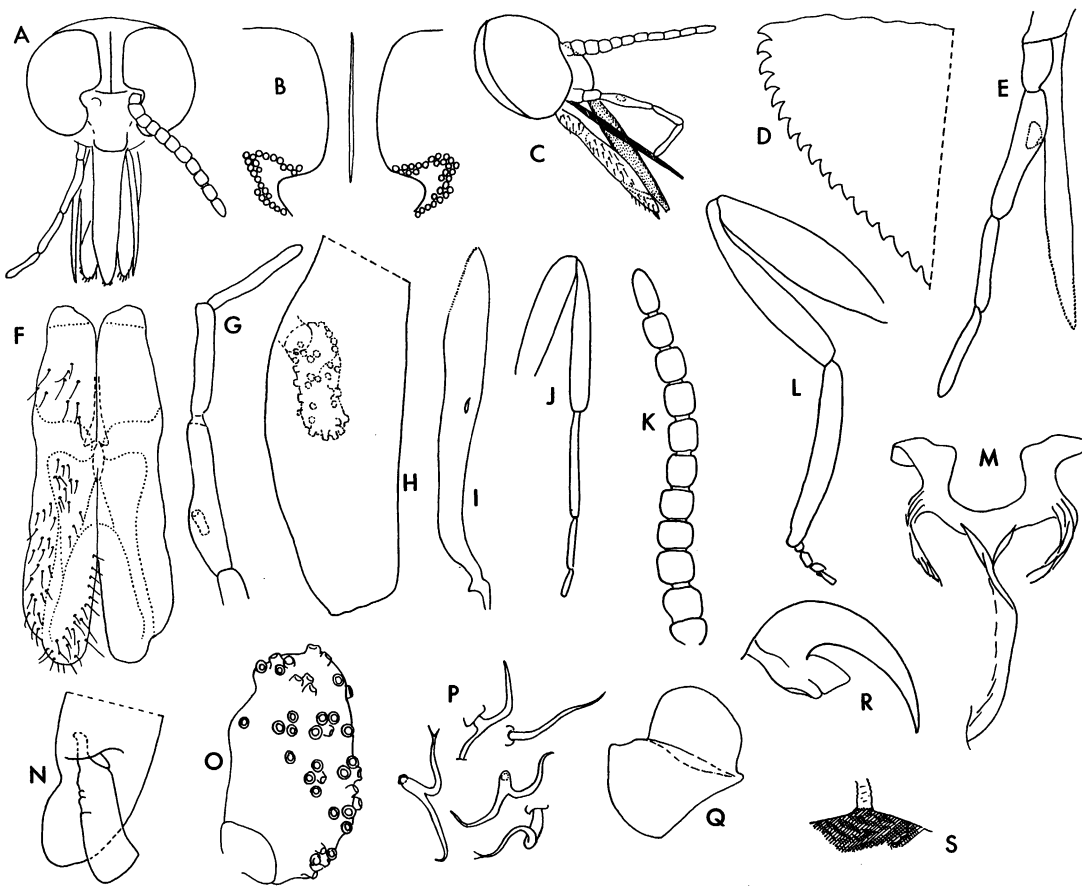

Fig. 157. *Gigantodax nasutus*. Female. **A.** Head with appendages, frontal view. **B.** Frons. **C.** Head, lateral view. **D.** Apex of mandible. **E.** Maxilla with palp. **F.** Labium. **G.** Maxillary palp. **H.** Basal portion of second article of maxillary palp. **I.** Mandible. **J.** Portion of foreleg. **K.** Antenna. **L.** Hind leg. **M.** Genital fork. **N.** Calcipala, with second tarsal segment. **O.** Sensory vesicle of of maxillary palp. **P.** Modified setae of VIII sternite of pupa. **Q.** Cercus and paraproct. **R.** Claw. **S.** Insertion of spermathecal duct on spermatheca.

Gill with five short, thick tubular branches, color whitish brown, surface minutely pitted, with minute, stellate, glabrous areas; respiratory filaments not observed (fig. 158A, B, D, F). General consistency of branches very delicate, collapsing when pupa is dried. All branches inserted individually on common base, constricted subbasally. First dorsal branch extending over dorsum of thorax of pupa; second branch U-shaped, basal half ascending, apical half descending; third and fourth branches directed forward; fifth branch U-shaped, basal half descending, second half ascending. Shape of frontoclypeus as illustrated (fig. 158C) with numerous heavily verrucose platelets arranged as in figure 158G. Facial trichomes hairlike, clypeus elongated. Thorax with heavily verrucose platelets arranged as in figure 158H. Thoracic trichomes hairlike, dorsolaterals more delicate than dorsocentral. Setae of abdominal tergite I hairlike, length 50–75 μm; setae of tergite II more spinelike, length 40–50 μm (fig. 158J). Tergites III and IV each with 4 + 4 short hooks (fig. 158L). Anterosublateral seta in shape of slender spine (fig. 158I). Setae of tergites V–VIII slender, length on tergite VII 55–65 μm. Spine-combs on tergites VI–VIII continuous or interrupted at center, consisting on tergite VII of 27 spines, length 20–30 μm, viz., half as long as setae of this tergite. Specialized setae of abdominal segments VIII

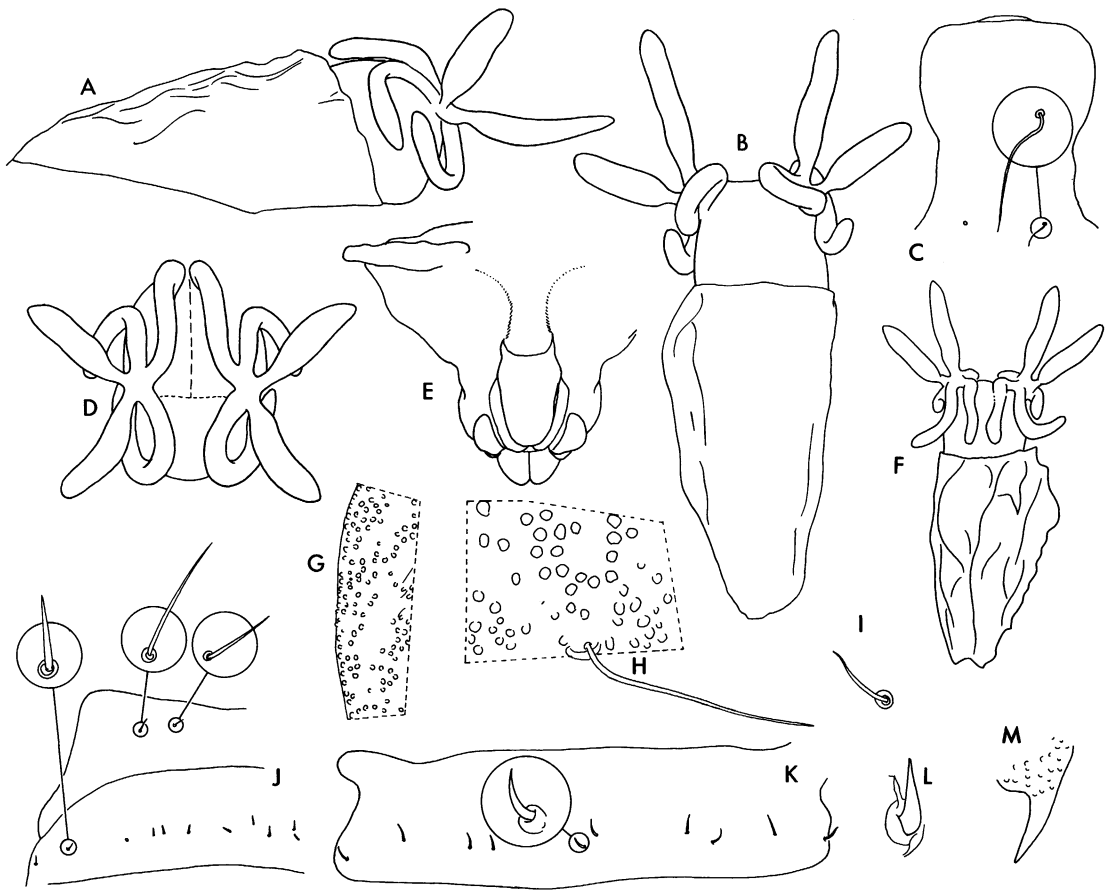

Fig. 158. *G. nasutus.* Pupa. **A, B.** Pupa in cocoon, lateral and ventral views, respectively. **C.** Frontoclypeus. **D.** Anterior portion of body with gills, frontal view. **E.** Portion of head sclerite. **F.** Pupa in dorsal view. **G.** Platelets on frontoclypeus. **H.** Thorax with platelets and trichomes. **I.** Anterosublateral trichome of abdominal tergite III. **J.** Chaetotaxy of abdominal tergites I and II. **K.** Sternite IV. **L.** Hook of tergite IV. **M.** Terminal spine of abdomen.

and IX variously curved or grapnel shaped (fig. 157P). Sternite IV (fig. 158K) with one median and 1 + 1 sublateral and 1 + 1 lateral similar setae. Sternite V with 3 + 3, VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous. Terminal hooks as in figure 158M.

Larva. Unknown.

HOLOTYPE: COLOMBIA: *Cundinamarca:* Alto de San Miguel, on road from Sibate to Fusagasuga, 2800 m, July 5, 1967 (P. and B. Wygodzinsky; AMNH), female (reared, and with associate pupal exuvia).

ADDITIONAL SPECIMENS: COLOMBIA: *Cundinamarca:* Paramo de Chisaca (or Sumapaz), S slope, 3700 m, July 2, 1965 (P. and B. Wygodzinsky; AMNH), 2 pupae.

ETYMOLOGY: The specific name is from the Latin *nasutus,* large nosed, for the unusually long proboscis of this species.

BIOLOGY: The few known pupae of *G. nasutus* were collected in very small, clear, shallow, slow flowing mountain streams, of a width not over 2 ft; in one stream where pupae were obtained (Sumapaz) the water temperature was 9°C. Pupae were located on the undersurfaces of stones.

DISCUSSION: The elongate mouthparts of the female of *nasutus* are found in no other species of *Gigantodax.* A comparable condition has been reported only in two species

of *Simulium* from New Guinea, *Simulium mafulense* Smart and Clifford and *S. rostrata* Smart and Clifford. The gills are superficially similar to those of *G. bettyae, septenarius,* and *horcotiani,* but *nasutus* differs from those species by the weak consistency of the gills, the lack of respiratory filaments, and the absence of cuticular processes on the apical portions of the gill branches, as well as by the shorter hooks on abdominal tergites III and IV.

Gigantodax rufescens (Edwards)
Figures 159A–Y, 160A–N, 161A–L

Simulium (*Gigantodax*) *rufescens* Edwards, 1931: 134. Orfila, 1935: 1528.
Gigantodax rufescens: Smart, 1945: 499. Wygodzinsky, 1949: 304. Vulcano, 1967: 3; 1977: 290.
Simulium rufescens: Vargas, 1945: 192.
Gigantodax wittmeri Wygodzinsky, 1951: 202. Coscarón and Wygodzinsky, 1962: 307. Vulcano, 1967: 4; 1977: 290. Coscarón, 1968: 65. NEW SYNONYMY.

DIAGNOSIS: Large species with yellowish imagos, without spines on R_1 and calcipala one-third length of second tarsomere, pupal gill with four wide, tubular, membranous branches, distinctly accuminate median and corner teeth, and gill histoblasts conspicuously wrinkled in larva.

REDESCRIPTION: *Female.* Length of wing 4.7–5.0 mm. Head slate gray, pilosity brass colored. Antenna and maxillary palp dark brown; scapus, pedicellus, and extreme base of first flagellomere orange, conspicuously contrasting with dark flagellum. Thorax light orange, setae golden colored. Wing translucent; veins orange. Setae on stem vein and on remaining veins golden colored, spinules black. Halter whitish. Legs from yellow to light orange; setae concolorous. Abdomen yellowish, disc of tergites mottled with darker pigment with hind margins narrowly white. Abdominal setae silver.

Frontal angle 30°. Fronto-ocular triangle higher than wide (fig. 159B). Shape and proportion of antennal segments as in figure 159A. Mandible with 24–25 teeth; outer margin faintly crenulated near apex. Maxilla with 26–29 teeth. Terminal segment of maxillary palp twice as long as preceding (fig. 159C). Second segment broadly oval, ratio length/width = 1:0.48–0.57. Sensory vesicle very large, neck distinct (fig. 159I). Sc with about 34 hairs. R and R_1 with setae in two or three irregular rows; spinules on R_1 absent in some cases, or several setae of R_1 converted, thickened, and shortened, but less so than spinules on C. R_s above with setae in one row, on lower surface in two or three irregular rows. A_1 almost reaching to wing margin. Shape and proportion of fore and hind leg segments as in figure 159E, F. Hind basitarsus 10 times as long as wide. Calcipala very short, not covering more than one-third of second tarsomere (fig. 159M). Basal tooth of claw unusually elongate (fig. 159D). Abdominal sternites with only delicate hairs. Genital fork and cercus with paraproct as illustrated (fig. 159K, L).

Male. Length of wing 4.6–4.7 mm. Color as in female. Holoptic. Shape and proportions of antennal segments as illustrated (fig. 159X); ratio length/width of first flagellomere 1:0.74–0.87. Apical segment of maxillary palp twice as long as penultimate (fig. 159R). Sensory vesicle narrowly elongate, with long neck (fig. 159J, Q); palpal ratio 1:0.30. Wing as in female. Shape and proportion of hind leg segments as in figure 159P. Fore basitarsus 9.1–10.9 times, hind basitarsus 7.0–7.8 times as long as wide (fig. 159N, O). Calcipala very short, only covering basal third of second tarsomere (fig. 159S–U). Distimere over two-thirds as long as basimere, with two apical spines (fig. 159V). Main body of ventral plate as long as wide (fig. 159Y). Hooks of endoparameral organ as in figure 159W.

Pupa. Cocoon very small, covering pupa ventrally to apex of pterotheca, extending dorsad only to third abdominal segment, leaving tergites I and II, thorax, head, and gills completely exposed (fig. 160A). Cocoon dark brown or piceous, not translucent, tightly woven but individual strands easily seen. Length of cocoon along dorsum 2.5–3.0 mm. Total length of the pupal body approximately 5 mm; cephalopterothecal length 2.9–3.1 mm. Gill each with four tubular, membranous, diverging branches perpendicular to longitudinal axis of body of pupa, apical half of branch forwardly directed (fig. 160A, D, E). Surface of branches microscopically dotted; no other cuticular structure perceptible. Respiratory filaments absent, not discernible even in gill histoblast of pharate pupa. Gill brown-

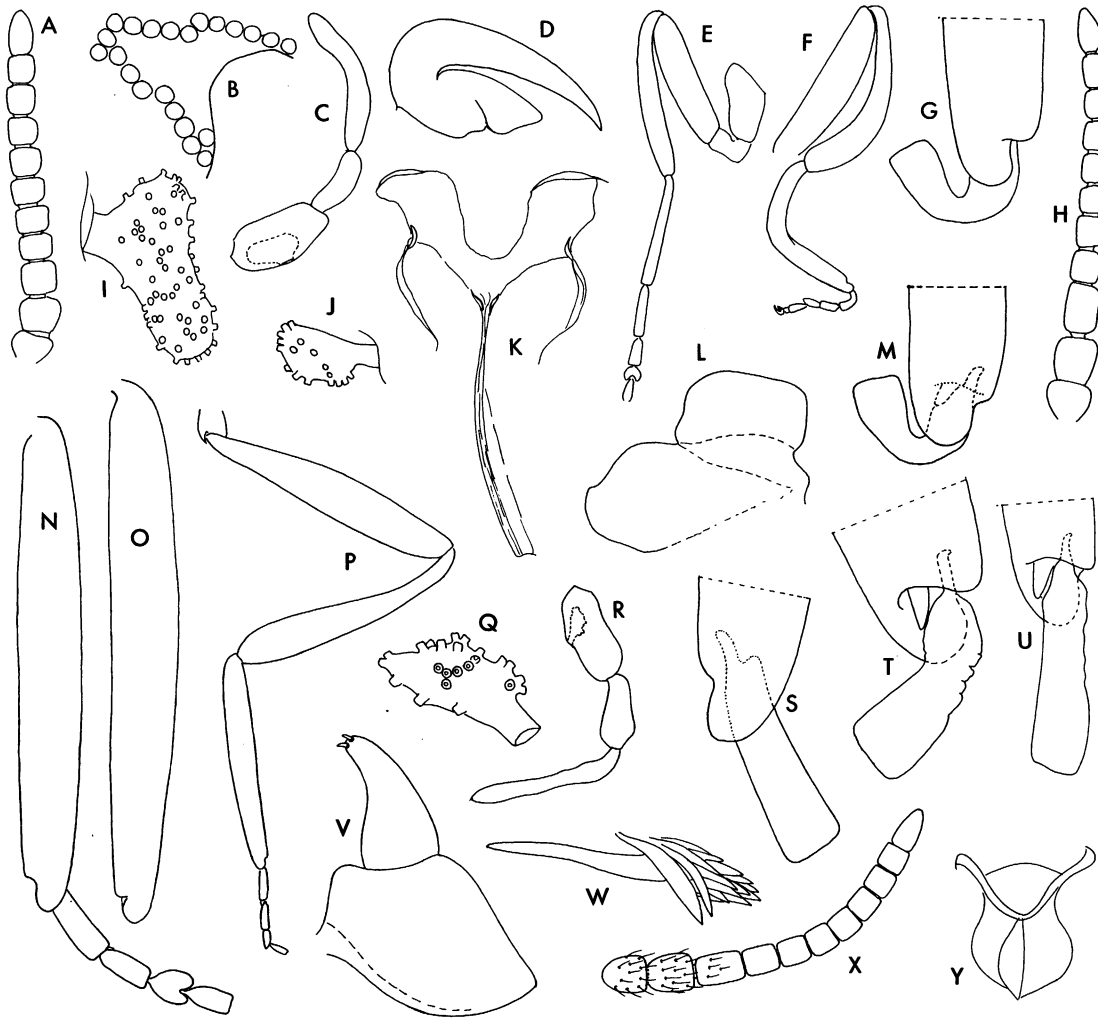

Fig. 159. *Gigantodax rufescens.* A–G. Female. **A.** Antenna. **B.** Fronto-ocular triangle. **C.** Maxillary palp. **D.** Claw. **E.** Foreleg. **F.** Hind leg. **G.** Calcipala with second tarsal article. **H.** Antenna of male, Copahue. **I.** Sensory vesicle of maxillary palp of female. **J.** Same, male. **K.** Genital fork. **L.** Cercus and paraproct. **M.** Calcipala of female, with second tarsal segment. **N.** Posterior tarsus, male type. **O.** Posterior basitarsus, male, Copahue. **P.** Hind leg, different male from Copahue. **Q.** Sensory vesicle of maxillary palp, male from Copahue. **R.** Maxillary palp, male. **S.** Calcipala and second tarsal segment, male type. **T.** Same, male, Copahue. **U.** Calcipala and second tarsal segment, male, Copahue. **V.** Basimere and distimere. **W.** Endoparamere. **X.** Antenna of male. **Y.** Ventral plate.

ish white, appearing polished. Gill delicate, branches collapsing when specimen is dried. Shape of frontoclypeus of female and male as in figure 160B, C, F, G; with numerous heavily verrucose platelets (fig. 160I) arranged as in figure 160N. Facial trichomes in shape of very delicate long hairs. Thorax with platelets on dorsal portion in distinct groups, forming in many cases small circles as in figure 160M. Dorsocentral and dorsolateral trichomes very delicate hairs. First and second abdominal tergites more distinctly tuberculate than remaining tergites. Setae of tergite I (fig. 160L) hairlike, very inconspicuous, and short (15–20 μm); setae of tergite II stronger and more elongate (up to 40 μm) (fig. 160H). Tergites III and IV each with 4 + 4 short hooks (fig. 160K). Anterodorsal seta absent.

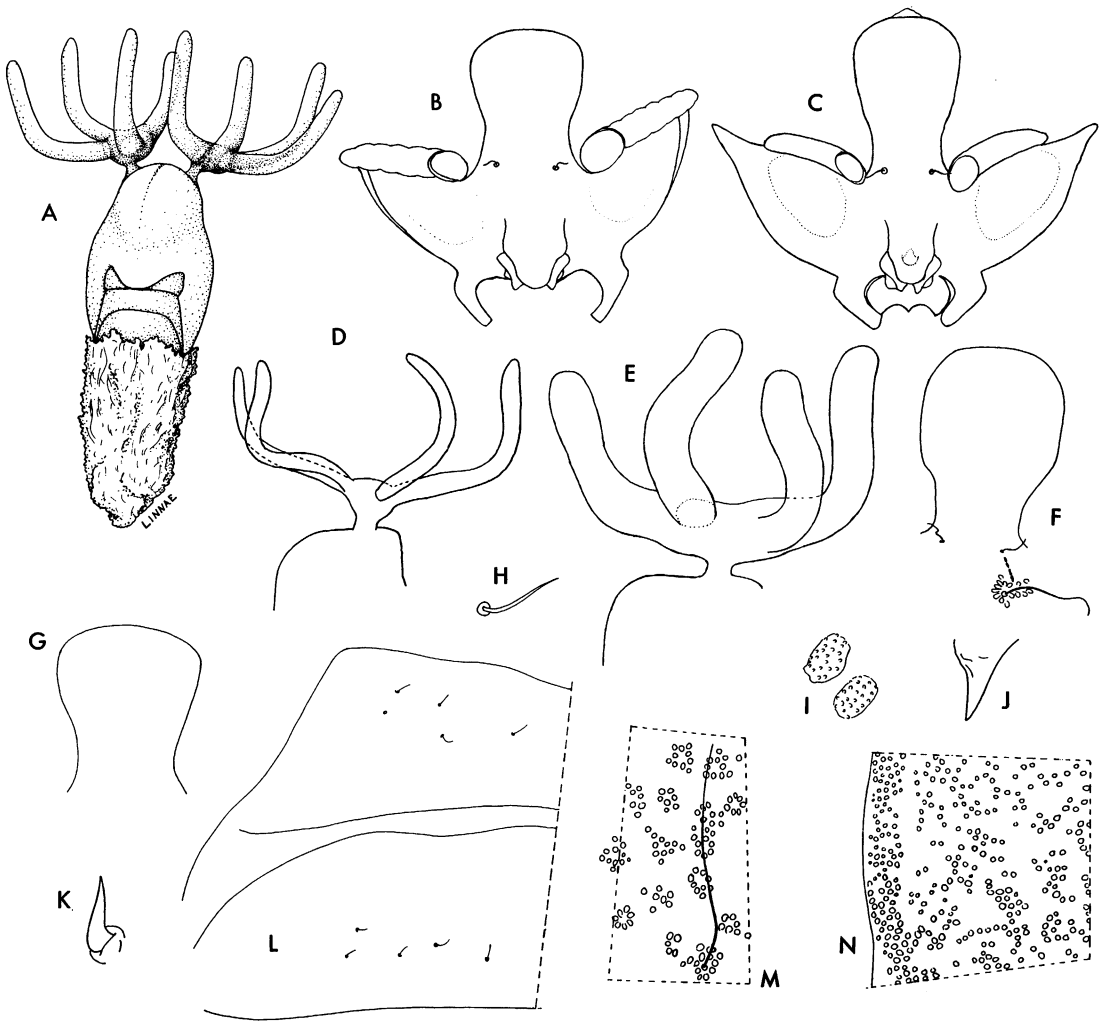

Fig. 160. *G. rufescens.* Pupa. **A.** Pupa in cocoon, dorsal view. **B.** Cephalic sclerite of female. **C.** Same, male. **D.** Teratological gills. **E.** Normal gills. **F.** Outline of frontoclypeus, male. **G.** Outline of frontoclypeus, female. **H.** Facial trichome. **I.** Platelets of thorax, high magnification. **J.** Terminal spine of abdomen. **K.** Hook of tergite IV. **L.** Chaetotaxy of abdominal tergites I and II. **M.** Thorax of male, with platelets and trichome. **N.** Distribution of platelets on frontoclypeus.

Setae of tergites V–VIII slender, length on tergite VIII 30–40 μm. Spine-combs on tergites VI–VIII continuous, consisting on tergite VII of 50–60 unusually small spines, length only 8–12 μm, viz., about one-third of length of setae of this tergite. Specialized setae of eighth and ninth segments simple, only slightly curved, few in number. Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous. Terminal hooks as in figure 160J.

Mature larva. Length 9.5–10.2 mm; width of head capsule 9.4–9.7 mm. Body shape usual for genus. Ventral papillae well developed. Color of larva from white to light brown, dorsal part of swollen posterior darkest. Head light brown; spots of cephalic apotome distinct (fig. 161A), but not strongly contrasting with general color of head. Hypostomial bridge slightly darker than rest of head capsule, with a median longitudinal recurrent whitish line (fig. 161B). Antenna shorter than stem of cephalic fan (fig. 161C), faintly pig-

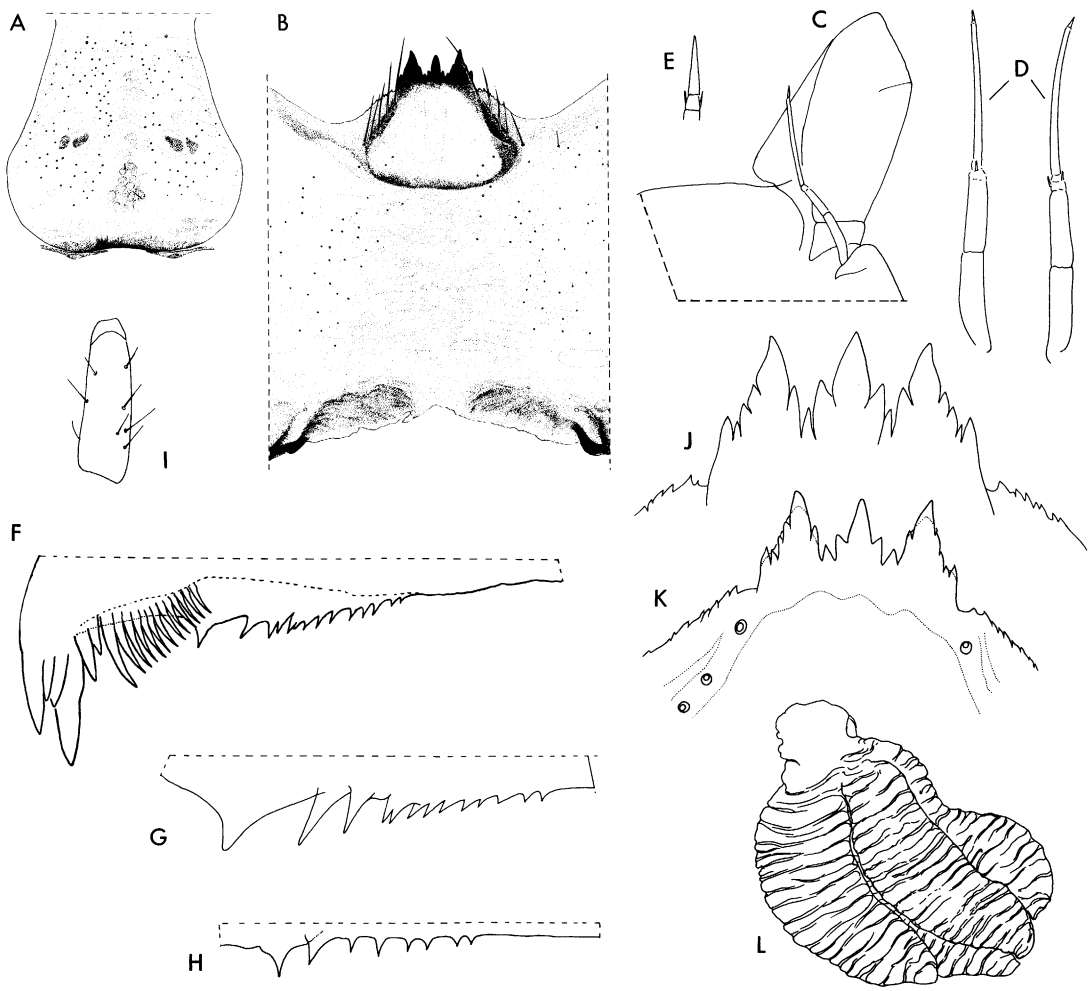

Fig. 161. *G. rufescens.* Larva. **A.** Cephalic apotome. **B.** Hypostomial bridge. **C.** Antenna and stem of cephalic fan. **D.** Antenna. **E.** Terminal sensillum of antenna. **F.** Apical portion and mandibular serrations of mandible. **G, H.** Mandibular serrations. **I.** Maxillary palp. **J, K.** Anterior portion of hypostomium. **L.** Gill histoblast.

mented, third segment not darker than first and second. Shape of antenna as in figure 161D; ratio of segments I–III = 1:0.67–0.80: 1.40–1.70; first and second segments combined from 9–10 times as long as width of second segment. Terminal sensillum five times as long as wide at base (fig. 161E). Cephalic fan with 30–40 large rays, their small teeth slightly decreasing in size within each group. Mandible (fig. 161F–H) with 10–15 inner teeth and 10–15 marginal serrations. Maxillary palp 2.8 times as long as wide at base (fig. 161I). Hypostomium as in figure 161J, K. Median tooth reaching level of corner tooth apex; line connecting apex of median tooth to apex to fourth lateral tooth intersecting other teeth. Line connecting apices of fourth lateral and corner teeth intersecting at an acute angle. Hypostomium with 7–11 lateral serrations and 4–5 hypostomial setae in each row. Gill histoblast as in figure 161L, conspicuously wrinkled, without trace of respiratory filaments, brown in mature specimens. Perianal scales well developed, very large, and strongly pigmented near upper arms of X-shaped sclerite, forming complete cir-

cumanal ring. Recurrent struts distinct but weakly pigmented. Crochet ring with 110–120 rows of 19–20 hooks each.

MATERIAL EXAMINED: ARGENTINA: *Tierra del Fuego:* Isla de los Estados, Arroyo Cook, Nov. 26, 1967 (A. Bachmann; INM), larvae; Ushuaia, Jan. 1960 (S. Coscarón and P. Wygodzinsky; AMNH), 1 larva. *Rio Negro:* Lago Mascardi, Feb. 15, 1967 (S. Coscarón; AMNH), 1 pupa; Cerro Catedral, 1700 m, Feb. 13, 1967 (S. Coscarón; AMNH), larvae; Arroyo Melgarejo, E of Lago Gutierrez, 800 m, Oct. 22, 1970 (S. Coscarón; AMNH), 1 pupa. *Neuquen:* Copahue, Jan. 1963 (S. Coscarón; AMNH and INM), various pharate adults of both sexes, pupae, and larvae. CHILE: *Malleco:* Curacautin, Rio Blanco, 1100 m, Feb. 1964 (L. Pena; CNC), 1 female. *Bio-Bio:* El Abanico, Dec. 31, 1950 (E. Ross and A. E. Michaelbacher; CAS), 1 male. *Talca:* Alto de Vilches, 1200 m, Oct. 30, 1969 (J. Rozen and L. Pena; AMNH), 1 female; ibid., Oct. 5–7, 1972 (S. Coscarón, L. Pena, and P. Wygodzinsky; AMNH), 1 male, 1 larva. *O'Higgins:* Pangal, Oct. 9, 1967 (S. Coscarón; AMNH), 1 pupa; Cajon del Maipo, Quebrada del Rio Colorado, 1200 m, Oct. 10, 1972 (L. Pena and P. Wygodzinsky; AMNH), 1 pupa. *Aconcagua:* Valle los Pinquenes, Feb. 7–12, 1964 (L. Pena; CNC), 1 female.

BIOLOGY AND DISTRIBUTION: *G. rufescens* prefers permanent streams that can be classified as "young" and "adolescent" by Dalmat's (1955) terminology. The aquatic instars of the species are in most cases found in rapids and small cascades, the larvae on the surfaces of rocks, the pupae on the upper or undersurfaces of large stones.

The species has an exceptionally wide range, extending from the central Chilean province of Aconcagua to the extreme south of Tierra del Fuego, a distance of more than 2500 km. In the northern part of its range (north of 40°S) the species occurs between 1000 and 1700 m altitude, but in Tierra del Fuego *rufescens* is found at or slightly above sea level. It had been reported before only from Argentina; the above records from Chile are the first for that country.

DISCUSSION: We have examined the male holotype of *Simulium* (*Gigantodax*) *rufescens* Edwards kept in the British Museum; its color and structural characters agree so well with those of *Gigantodax wittmeri* Wygodzinsky that we find it necessary to synonymize the latter species.

Superficially, the pupa of *rufescens* resembles that of *G. nasutus,* on account of the small number of the structurally quite similar tubular gill branches, which collapse when dry, in both species. However, the general arrangement of the gill branches is quite different in the two species, and there are no characters in the female (males and larvae are not known for *nasutus*) that would suggest a close relationship.

Superficially, the adults of *G. rufescens* are very similar to those of *G. shannoni* with which they share the overall light color, including the setae of the stem vein, but *rufescens* can easily be distinguished from *shannoni* by the very short calcipala, which is quite long and thin in *shannoni.* Pupal gills and larval hypostomial shapes also permit differentiation of the two species.

Coscarón and Wygodzinsky (1962) described a male and a female pupa of *rufescens* (as *wittmeri*) distinguished from each other by the conspicuously different thickness of their gill branches; the authors postulated the possibility of sexual dimorphism. We have now examined a considerable number of pupae of both sexes and have been unable to confirm that hypothesis; all specimens are approximately as in figure 160E and in the original description of *G. wittmeri* (Wygodzinsky, 1951: fig. 40). The specimen with very thin gill branches illustrated by Coscarón and Wygodzinsky (1962: fig. 109) must be considered as abnormal. The basal tooth of the female claw and the larval hypostomial dentition of *G. rufescens* are abnormal for the *wrighti* group.

Gigantodax dryadicaudicis, new species

Figures 162A–P, 163A–E, 164A–M

DIAGNOSIS: Distinguished from all congeneric species by a wealth of characters, such as the long, drawn-out female paraprocts, beset on their apex with numerous strong elongate setae, the trunklike main branches of the gill of the pupa, and in the larva, by the mandibular serrations, which are reduced to one or two.

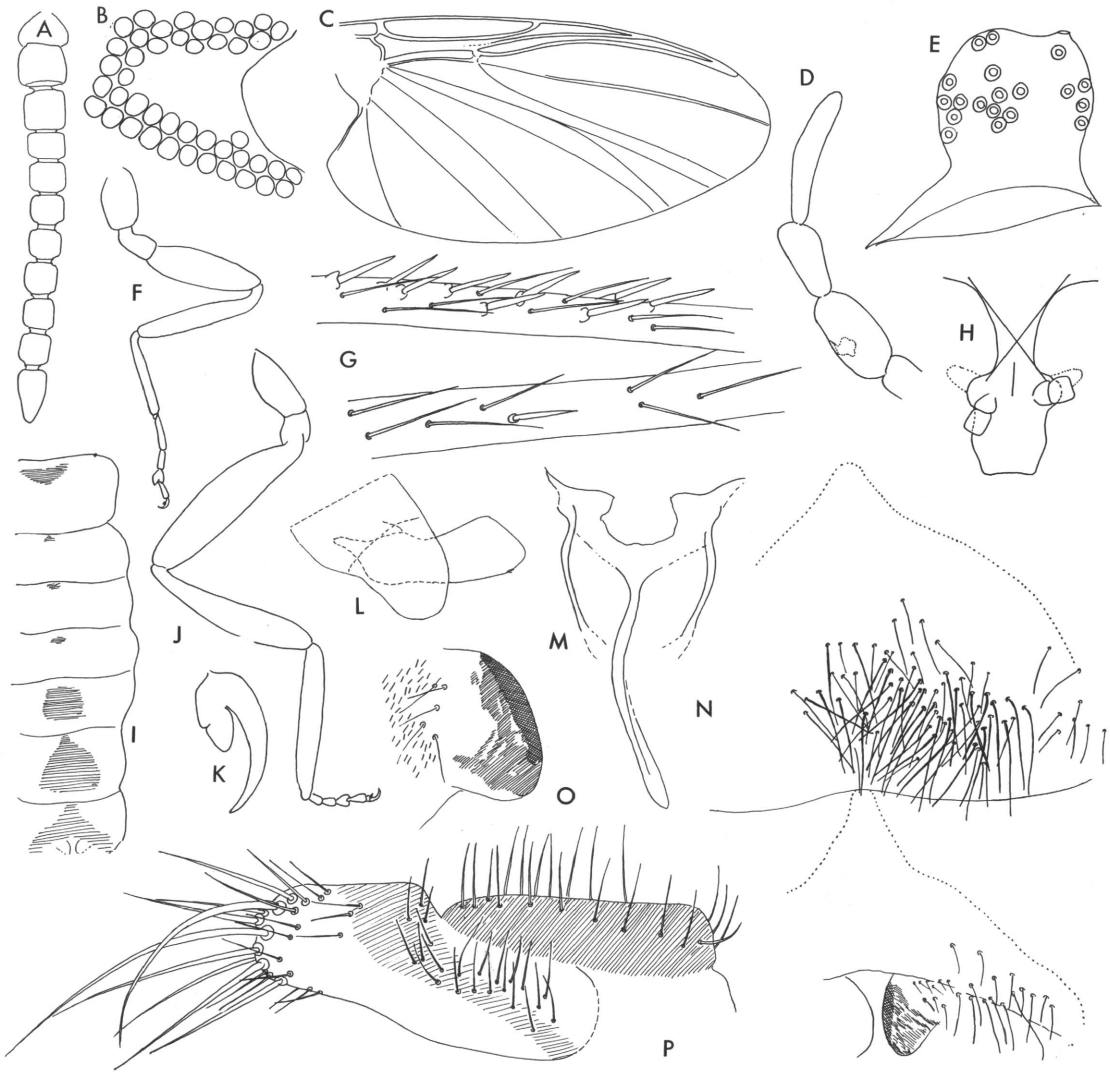

Fig. 162. *Gigantodax dryadicaudicis.* Female. **A.** Antenna. **B.** Fronto-ocular triangle. **C.** Forewing. **D.** Maxillary palp. **F.** Foreleg. **G.** Detail of wing. **H.** Frons. **I.** Under surface of abdomen, with sclerotized plates. **J.** Hind leg. **K.** Claw. **L.** Calcipala, with second tarsal segment. **M.** Genital fork. **N.** Sternites VII and VIII, with gonapophyses. **O.** Gonapophyses. **P.** Cercus and paraproct.

DESCRIPTION: *Female.* Length of wing 3.5 mm. Head gray, with scattered setae, from brass colored to silvery. Mouth parts dark brown. First three antennal segments orange colored, remaining segments dark brown. Scutum orange, with short brass-colored pilosity. Metanotum pale yellow, with delicate silvery pruinosity, and long, erect brown or yellow setae. Pleural region reddish brown with brass-colored setae. Wings translucent, veins light brown. Hairs on stem vein and basal tuft brass colored. Legs very light yellowish brown, extremity of articles darkened, especially on tarsus. First abdominal segment yellowish, remainder dark gray; setae of abdomen brass colored.

Frontal angle 75° (fig. 162H). Fronto-ocular triangle (fig. 162B) higher than wide. Antenna as in figure 162A. Mandible with 32–35 well-developed teeth on both margins.

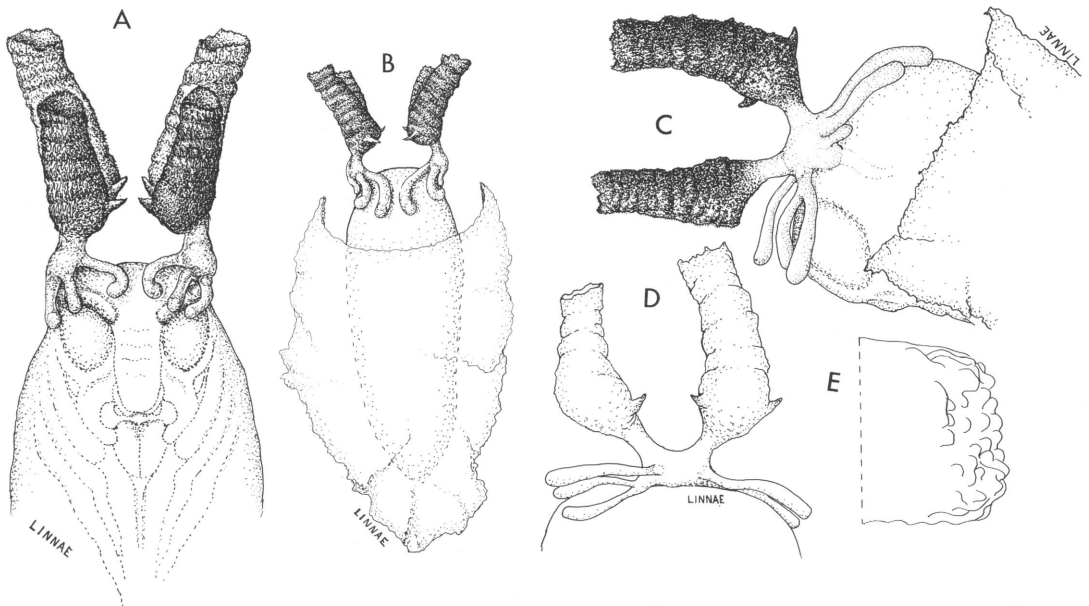

Fig. 163. *G. dryadicaudicis.* Pupa. **A.** Anterior portion of pupa, under surface. **B.** Pupa in cocoon, dorsal view. **C.** Anterior portion of pupa, side view. **D.** Gill, lateral view. **E.** Apex of small gill branch, high magnification.

Maxilla with 25 teeth. Maxillary palp (fig. 162D) with apical segment slightly less than twice as long as penultimate. Second segment of palp oval, ratio length/width = 1:0.35–0.42. Sensory vesicle (fig. 162D, E) unusually small, subglobular. A_1 reaching wing margin (fig. 162C). Sc with 19–20 hairs. Setae on R in one or two, on R_1 in two or three irregular rows (fig. 162G), without spinules. R_s without spinules, with setae in one row on apical portion of dorsal surface, two or three irregular rows over entire extension of undersurface of vein. Shape and proportions of fore and hind leg segments as in figure 162F, J. Hind basitarsus six times as long as wide. Calcipala (fig. 162L) covering over half the length of second tarsomere. Basal tooth of claw as in figure 162K.

Abdominal sterna (fig. 162I) membranous, with small to minute median sclerotized areas. Eighth sternite (fig. 162N) with patch of numerous long and strong setae on posterior portion. Gonapophyses (fig. 162N, O) short, glabrous, partially pigmented. Genital fork with slender stem and arms (fig. 162M). Cercus and paraproct (fig. 162P) extraordinarily compressed dorsoventrally; paraprocts apically with a group of long, strong setae. Spermatheca with scattered spicules, single or in pairs.

Male. Unknown.

Pupa. Cocoon extending to anterior declivity of body, leaving head and gills exposed, anterior margin distinctly reinforced (fig. 163A–C). Cocoon light brown, tightly woven but translucent when not covered by foreign matter. Length of cocoon along dorsum 2.7–3.0 mm. Total length of pupa without gills 2.5–3.0 mm; cephalopterothecal length 2.0 mm. Gill (fig. 163A–E) brown, rigid, each consisting of two large, forward-directed arms, one dorsal and one ventral, and five short tubular branches, two dorsal and three ventral, closely adhering to surface of thorax. Large pedunculate arms, subcylindrical, slightly tapering toward apex, heavily rugose and slightly pigmented. Dorsal arm near base with two short spinelike processes, ventral arm with one. Head without platelets. Shape of frontoclypeus of pupa as in figure 164D. Facial trichomes long, hairlike; no other trichomes present. Thorax with minute tubercles, trichomes of thorax as in figure 164A, B. Setae of first abdominal tergite hair-

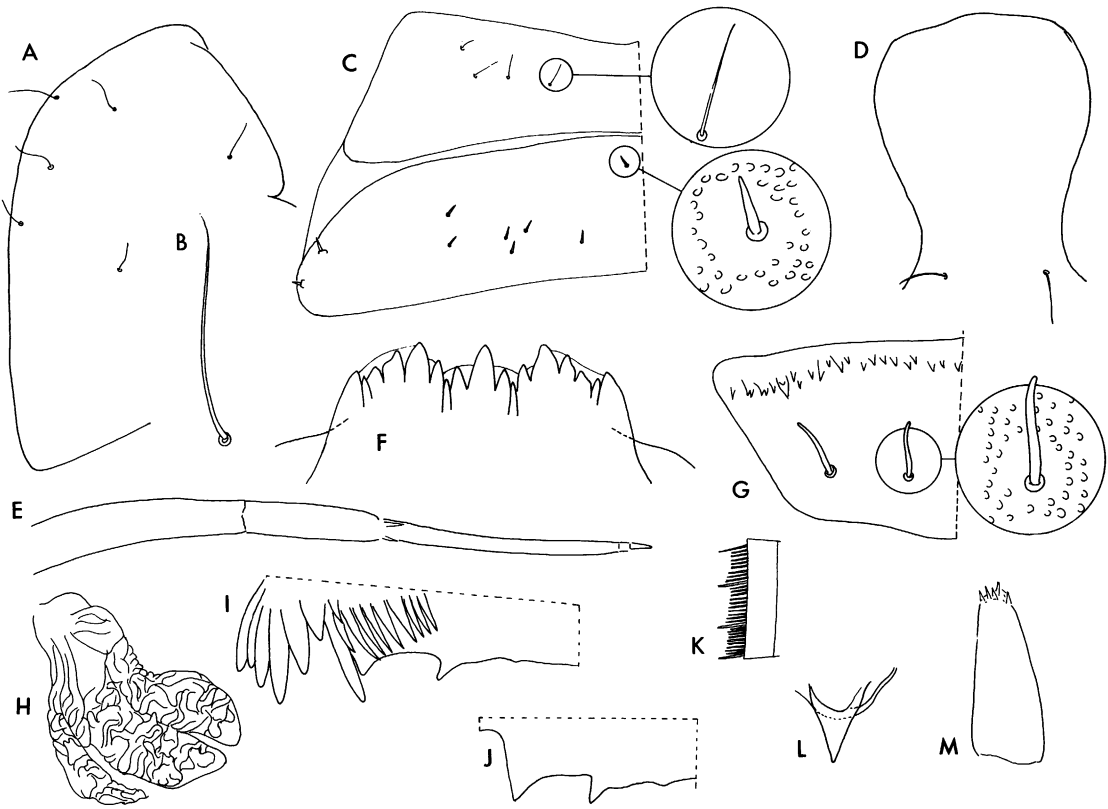

Fig. 164. *G. dryadicaudicis.* **A.** Portion of thorax, with trichomes. **B.** Trichome of thorax of pupa. **C.** Chaetotaxy of abdominal tergites I and II. **D.** Frontoclypeus of female pupa. **E.** Antenna. **F.** Anterior portion of hypostomium. **G.** Detail of tergite VIII of pupa. **H.** Gill histoblast, slightly opened. **I.** Apex of mandible. **J.** Mandibular serration. **K.** Teeth of ray of cephalic fan. **L.** Apical spine of abdomen. **M.** Maxillary palp.

like (fig. 164C), length 60–70 μm. Setae of second tergite spinelike, about 20 μm long. Tergites III and IV each with 4 + 4 hooks (fig. 164G). Setae of tergites V–VIII slender, length on tergite VII about 60 μm, those of tergite VIII as in figure 164G. Spine-combs on tergites V–VIII irregularly arranged, on tergite VII with approximately 18 simple or apically bifid spines, length 18–20 μm, less than the length of the setae of this tergite. Specialized setae of terminal segment few in number. Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; single hooks also present in pleural membrane of segments VI and VII. Sternite VIII glabrous. Terminal spine short (fig. 164L).

Mature larva. Length 5 mm; width of head capsule 0.5 mm. Body shape normal for the genus. Ventral papillae not examined. Shape of antenna as in figure 164E. Ratio of length of antennal segments I–III = 1:0.59–0.68: 1.24–1.57. Terminal sensillum about 3.5 times as long as wide. Cephalic fan with 32–35 large rays; combs as in figure 164K. Mandible with only one or two marginal serrations (fig. 164I, J) and 9–10 inner teeth. Maxillary palp (fig. 164M) about twice as long as wide at base. Hypostomium as in figure 164F. Median tooth slightly below level of corner tooth apex; line connecting apices of median tooth and fourth lateral tooth intersecting several other teeth. Line connecting apices of fourth lateral tooth and corner tooth meeting at angle of 150°. Hypostomium with lateral serrations obsolescent; 6–7 hypostomial setae in single row. Cervical sclerites as in *G.*

cormonsi. Histoblast as in figure 164H; large branches appearing darker than short branches. Perianal scales not observed. Recurrent struts not developed. Crochet ring with about 120 rows of approximately 25 hooks each. Rectal gills not observed.

Holotype. CHILE: *Talca:* Alto de Vilches, 1200 m, Oct. 5–7, 1972 (S. Coscarón, L. Pena, and P. Wygodzinsky; AMNH), female with pupal skin.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 2 females with their pupal skins, paratypes, 5 pupae, one larva. ARGENTINA: *Neuquen:* Hua-Hum, Jan. 28, 1979 (S. Coscarón; MLP), 1 pupa.

ETYMOLOGY: From the Greek *Dryas,* a woodnymph, and the Latin *caudex-icis,* stem, trunk, in reference to the gills' appearance.

DISCUSSION: This is a peculiar species with characters as explained in the diagnosis that permit easy separation from all others. It differs from other species of the *wrighti* group by the presence of a small sensorial organ on the maxillary palp, very elongate cercus, and paraproct with stout trichomes in the female, and reduction of marginal serrations in the larval mandible.

Gigantodax incapucara, new species
Figures 165A–R, 166A–L

DIAGNOSIS: The species is characterized by the wide tongue-shaped branches of the pupal gills.

DESCRIPTION: *Pharate female.* Wing length about 4 mm. Color of scutum light reddish brown (possibly darker in fully developed specimens); pilosity of scutum golden yellow.

Frontal angle 40°. Fronto-ocular triangle (fig. 165D) about as long as wide. Shape and proportions of antennal segments as in figure 165A. Mandible with teeth only on inner margin, their number not established. Maxillae with 26–27 teeth. Last segment of maxillary palp only slightly longer than penultimate (fig. 165B). Second segment of maxillary palp elongate, ratio length/width = 1:0.36–0.42. Sensory vesicle of maxillary palp comparatively small, with short neck (fig. 165D); Sc with 19 hairs. R with setae in two irregular rows. R_1 with very numerous spinules, much more numerous than setae (fig. 165E), beginning at or slightly below level of insertion of Sc on C. R_s with setae in two rows (one each on concave and convex portion of vein), convex portion with one or two setae transformed into spinules similar to those on R_1 (observation on one wing only). A_1 reaching to wing margin. Shape and proportions of fore and hind leg segments as in figure 165F, I. Hind basitarsus about 8.2 times as long as wide. Calcipala extending very close to apex of second tarsomere (fig. 165R). Basal tooth of claw as in figure 165G. Abdominal sternites with delicate setae only. Cercus, paraproct, and genital fork as in figure 165H, J.

Male (pharate). Color of scutum as in female, but slightly darker. Wing length about 3.5 mm. Sc with 16 setae; R_1 with spinules beginning basad of level of insertion of Sc with C. Fore basitarsus 9.5 and hind basitarsus about 7.5 times as long as wide. Calcipala wider than long, and three-fourths length of second tarsomere. Basimere subtrapezoidal; distimere subtriangular, about half the length of basimere and with two apical spines. Ventral plate longer than wide, without distal concavity. Aedeagus membrane without spines, and endoparameral organ with strong hooks.

Pupa. Cocoon covering pupa to center of thorax dorsally, somewhat more advanced on sides and below (fig. 166A). Length of cocoon along dorsum, 3.0 mm, at sides 3.5 mm. Gills consisting each of two medium-size and one very small dorsal and one medium-size ventral tubular branch, in addition to two very large, dorsoventrally flattened, tongue-shaped anterolateral branches (fig. 166A, B). Basal portion of branches with minute, dotted cuticular projections (fig. 166F, J), apical portion heavily and irregularly rugose (fig. 166H). Respiratory filaments (some observable in gill histoblast) caducous. Shape and proportions of frontoclypeus as in figure 166C, with numerous, irregularly scattered, verrucose platelets (fig. 166L). Facial trichomes (not well preserved) probably spinelike. Thorax with platelets numerous, verrucose, scattered or arranged in irregular clusters (fig. 166I), dorsocentral and dorsolateral trichomes numbering four or five, slender hairlike, very inconspicuous. Setae of abdominal tergite I hairlike, length 38–45 μm; setae of tergite II spinelike, much shorter, 18–20 μm long (fig. 166G). Tergites III and IV

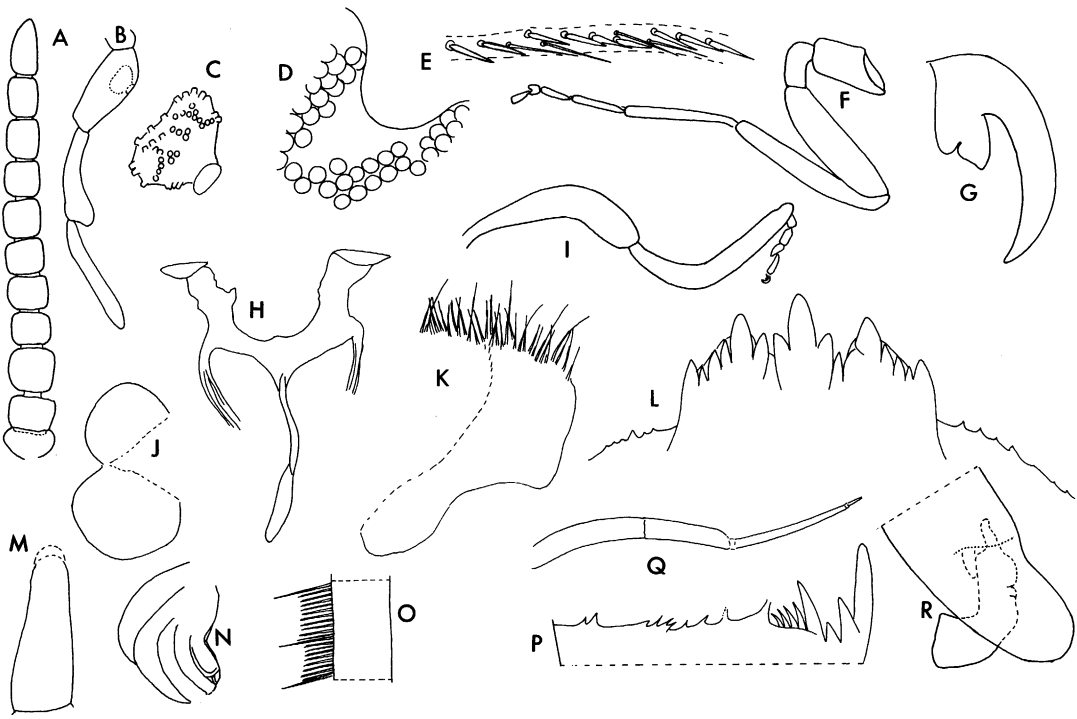

Fig. 165. *Gigantodax incapucara.* A–J. Female. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle of maxillary palp. **D.** Fronto-ocular triangle. **E.** Section of R_1. **F.** Foreleg. **G.** Claw. **H.** Genital fork. **I.** Hind leg. **J.** Cercus and paraproct. K–P. Larva. **K.** Lateral sclerite of proleg. **L.** Anterior pattern of hypostomium. **M.** Maxillary palp. **N.** Gill histoblast. **O.** Detail of teeth of rays of cephalic fan. **P.** Apex of mandible. **Q.** Antenna. **R.** Calcipala.

each with 4 + 4 short hooks (fig. 166D). Anterosublateral setae spiniform (fig. 166K). Setae of tergites V–VIII slender, inconspicuous, length on tergite VII about 30 μm. Spinecombs on tergites VI–VIII continuous, on tergite VII of about 40 spines, their length 5–10 μm, viz., not over one-third of length of setae of this segment. Specialized setae of segments VIII and IX slightly curved, some bifurcate (fig. 166E). Sternite IV with three distinct groups of two small hooks each, one group median and 1 + 1 sublateral. Sternite V with 3 + 3, VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 6.8–8.7 mm. Body shape as usual for the genus; ventral papillae well developed. Color of larva faintly brownish, due to uniformly deposited hypodermal pigment, except on undersurface of posterior, swollen portion of body. Head yellowish; spots of cephalic apotomes conspicuous. Hypostomial bridge slightly but perceptibly darkened, with light colored, median longitudinal line. Antenna approximately as long as stem of cephalic fan, faintly pigmented, third segment not darker than preceding. Shape of antenna as in figure 165Q; ratio of segments I–III = 1:0.7:1.0. Terminal sensillum about 4.5 times as long as wide. Cephalic fan with about 33 large rays, teeth as in figure 165O; small teeth rather uniform in size. Mandible with 10 inner teeth and 10 marginal serrations (fig. 165P). Maxillary palp about three times as long as wide at base (fig. 165M). Hypostomium as illustrated (fig. 165L). Median tooth projecting beyond level of corner tooth apex; line connecting apices of median and fourth lateral teeth intersecting corner tooth. Hypostomium with six to eight lateral serrations and five hypostomial setae. Cervical sclerites as in *G. cormonsi.* Lateral sclerite of proleg as in figure 165K. Gill histoblast as in figure 165N. Perianal scales well developed, forming complete cir-

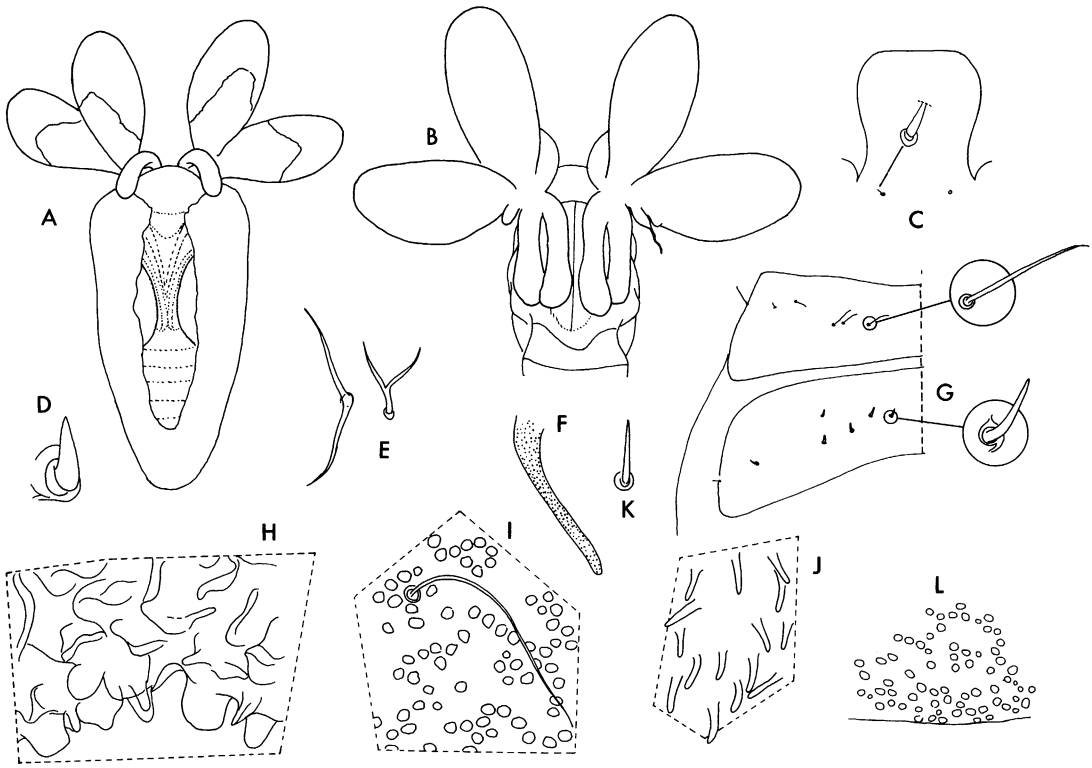

Fig. 166. *G. incapucara.* Pupa. **A.** Pupa, seen from below. **B.** Anterior portion of pupa, seen from above. **C.** Frontoclypeus of female pupa. **D.** Hook of abdominal tergite III. **E.** Setae of terminal segments. **F.** Detail of respiratory filament. **G.** Chaetotaxy of abdominal tergites I and II. **H.** Detail of surface structure of large gill branches. **I.** Thoracic trichome. **J.** Detail of surface structure of tubular gill branches. **K.** Anterosublateral trichome of abdominal tergite III. **L.** Distribution of platelets of frontoclypeus.

cumanal ring. Recurrent struts heavily sclerotized.

HOLOTYPE: PERU: *Cuzco:* Machu Picchu, 2070 m, April 18, 1971 (S. Coscarón; MLP), female (with its associated pupal exuviae).

ADDITIONAL SPECIMENS: Same data as holotype: two larvae. BOLIVIA: *Cochabamba:* El Sillar 2870 m, Nov. 15, 1977 (S. Coscarón; AMNH), 1 pharate male, 3 pupae, several larvae.

ETYMOLOGY: The specific name is taken from the Quechua *inca,* an Inca, a noble, and *pucara,* a fortress. Machu Picchu, where this species was found, is considered by some to have been an Inca fortress.

BIOLOGY. The aquatic instars of *G. incapucara* were found together with those of other species of the genus, in a temporary rivulet running down a slope above the road near the Machu Picchu hostelry.

DISCUSSION: *G. incapucara* is possibly related to *G. impossibilis,* with which it shares several apomorphies, such as the highly, although somewhat differently, modified pupal gills, the comparatively short sensory organ of the maxillary palp of the female, the hair-like thoracic trichomes, the presence of three pairs of small hooks on abdominal sternite IV of the pupa, and the general structure of the hypostomium of the larva. The most striking autapomorphic characters of *G. incapucara* are, of course, the structure of the pupal gill as well as the very large number of spinules on R_1, with occasional spinules appearing even on R_s.

Gigantodax herreri, new species
Figures 167A–T, 168A–V

Gigantodax bolivianum: Wygodzinsky, 1958: 140 (*nec* Enderlein).

DIAGNOSIS: The structure of the globose gills of the pupa is sufficient to distinguish

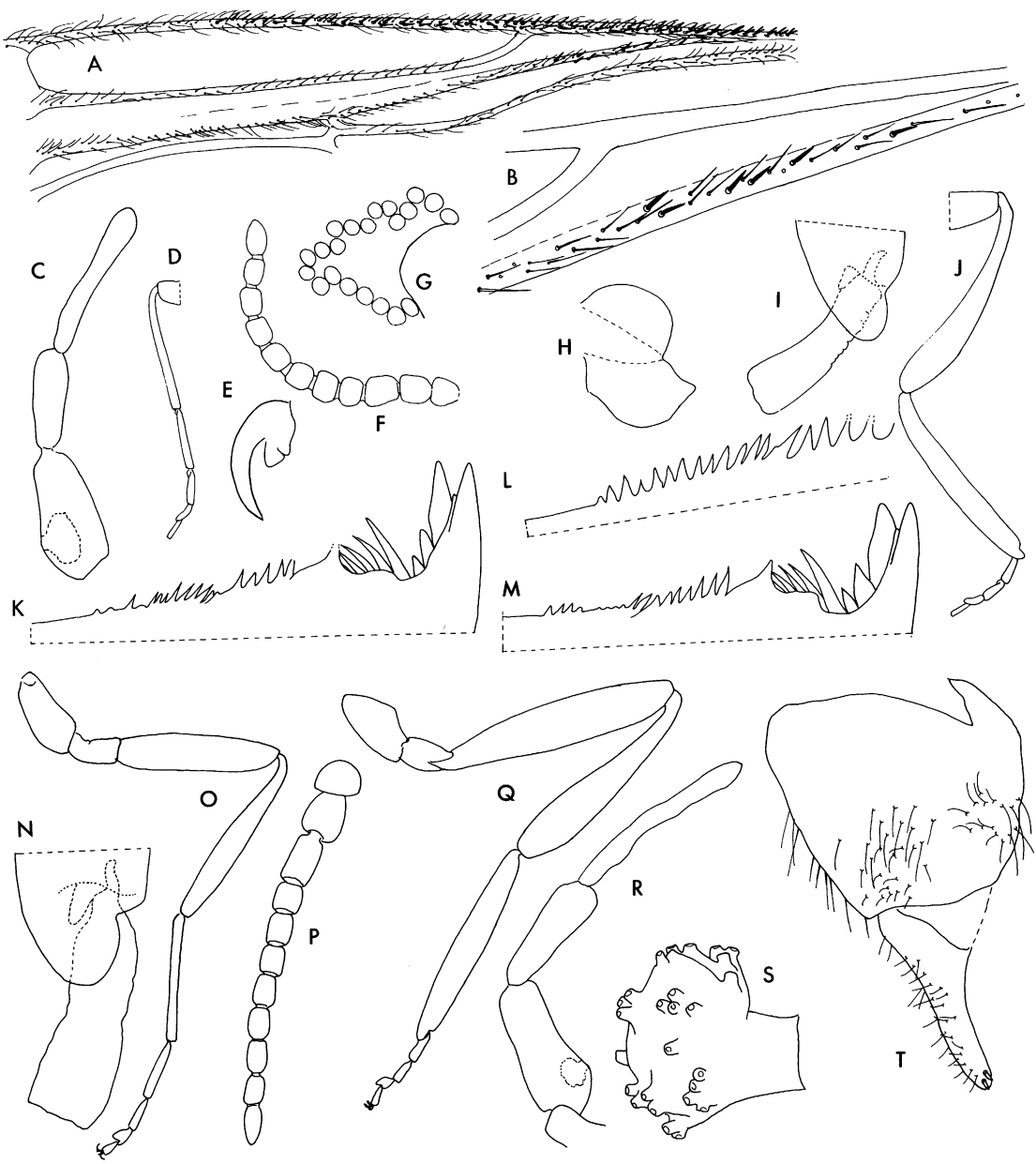

Fig. 167. *Gigantodax herreri.* **A.** Anterior portion of wing. **B.** Portion of R. C–J. Female. **C.** Maxillary palp. **D.** Foreleg. **E.** Claw. **F.** Antenna. **G.** Fronto-ocular triangle. **H.** Cercus and paraprocts. **I.** Calcipala, with second tarsal segment. **J.** Hind leg. **K.** Apex of mandible of larva. **L.** Marginal serrations of mandible. **M.** Apex of different mandible. N–T. Male. **N.** Calcipala with second tarsal segment. **O.** Foreleg. **P.** Antenna. **Q.** Hind leg. **R.** Maxillary palp. **S.** Sensory vesicle of maxillary palp. **T.** Basimere and distimere.

this species from all others included in the genus.

DESCRIPTION: *Female.* Length of wing 4.9–5.4 mm. Head dark gray; pilosity silvery, rarely brass colored. Antenna dark gray; scapus, pedicellus, and basal portion of first flagellomere orange. Scutum extremely variable in color, from pale grayish brown to rust brown or even piceous; dark median region in some specimens limited on each side by

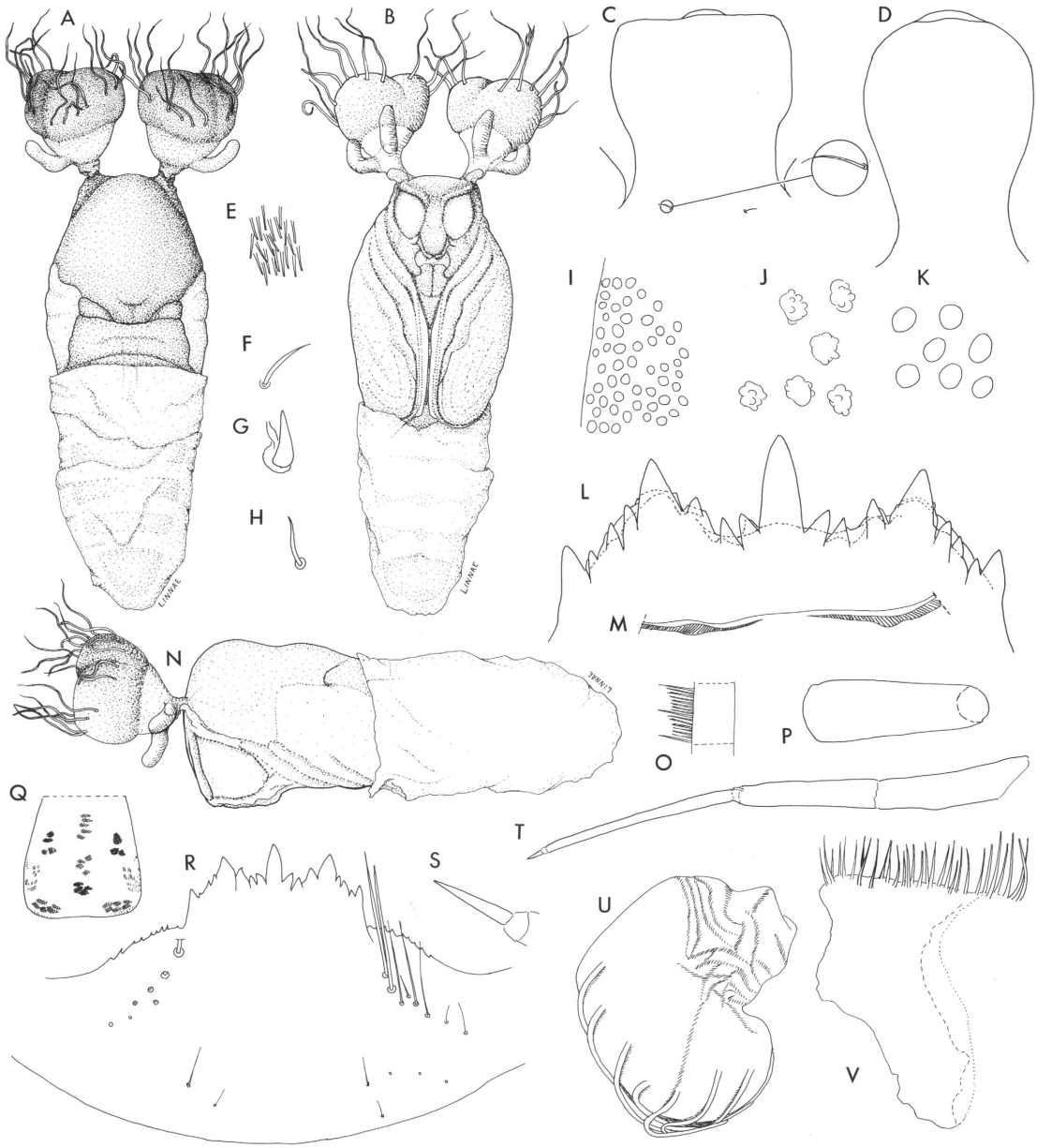

Fig. 168. *G. herreri.* **A, B.** Pupa in cocoon. A. Dorsal view. B. Under surface. **C.** Frontoclypeus, female pupa. **D.** Same, male pupa. **E.** Microstructure of globose portion of gill. **F.** Seta of abdominal tergite II of pupa. **G.** Hook of tergite IV of pupa. **H.** Anterosublateral trichome of abdominal tergite III. **I.** Platelets of frontoclypeus of pupa. **J.** Platelets of frontoclypeus of pupa in detail. **K.** Platelets of thorax of pupa. **L.** Anterior portion of hypostomium. **M.** Cervical sclerites. **N.** Pupa with cocoon, side view. O–V. Larva. **O.** Teeth of ray of cephalic fan. **P.** Maxillary palp of larva. **Q.** Cephalic apotome. **R.** Hypostomium. **S.** Apical sensillum of antenna. **T.** Antenna. **U.** Gill histoblast. **V.** Lateral sclerite of proleg.

narrow light-colored line. Scutellum and metanotum from light reddish brown to pi-

ceous. Setae of thorax from brass colored to golden yellow. Pleural region from light to

dark reddish brown, with faint darkish pollinosity. Wing translucent; veins yellowish brown. Setae on stem vein dark, with distinct golden or reddish tingle; remaining wing setae dark. Halter very light yellowish brown. Legs light brown. Abdominal fringe and remaining hairs of abdomen from silvery to golden yellow. Abdominal tergites piceous, with hind margins narrowly whitish.

Frontal angle 55–60°. Fronto-ocular triangle about as high as wide (fig. 167G). Shape and proportions of segments of antenna as in figure 167F. Mandible with 30–34 teeth. Maxilla with 28–34 teeth. Apical segment of maxillary palp about twice as long as penultimate (fig. 167C). Second segment of maxillary palp suboval and sensory vesicle well developed, with short but distinct neck. Sc with 23–32 hairs (fig. 167A), R and R_1 with setae arranged in two or three irregular rows. Spinules on R_1 present, beginning at or apical to level of insertion of Sc on C, much less numerous than hairs (fig. 167B). R_s with setae in two rows. A_1 almost reaching wing margin. Shape and proportions of leg segments as in figure 167D, J. Hind basitarsus 7.5–8.0 times as long as wide. Calcipala falling short of level of center of second tarsomere (fig. 167I). Basal tooth of claws as in figure 167E. Abdominal sterna with only delicate hairs. Genital fork (incorrectly represented in Wygodzinsky, 1958: fig. 101) similar to that shown in figure 169A; cercus and paraproct as illustrated (fig. 167H).

Male. Length of wing 4.6–4.8 mm. Color as variable as in, and similar to, female, but hairs in all specimens examined yellowish white.

Holoptic. Shape and proportions of antennal segments as in figure 167P; ratio length/width of first flagellomere 1:0.59–0.65. Terminal segment of maxillary palp conspicuously longer than penultimate (fig. 167R). Sensory vesicle subglobular, with distinct neck (fig. 167S). Wing much as in female. Shape and proportions of fore and hind leg segments as in figure 167O, Q. Fore basitarsus 13–15 times, hind basitarsus 6.8 times as long as wide. Calcipala short, not reaching level of center of second tarsomere (fig. 167N). Distimere elongate, almost as long as basimere, conspicuously narrowed on apical half, with two distal spines (fig. 167T). Main body of ventral plate as long as wide.

Pupa. Cocoon very small, sleevelike, covering only abdomen, in many cases leaving two anterior segments exposed; thorax, head, and gills free (fig. 168A, B, N). Color of cocoon very light brown, almost whitish, tightly woven but translucent; cocoon appearing polished when examined in liquid. Length of cocoon along dorsum 2.0–3.0 mm. Total length of body of pupa 4.0–5.0 mm; cephalopterothecal length 2.8 mm. Gills each with one large dorsal subglobular structure, and two short, stout somewhat curved, subcylindrical branches and basal half of subglobular portion microscopically dotted, but appearing highly polished under low magnification, color of these areas ivory when dry (fig. 168A, B, N). Surface of apical portion of subglobular structure with extremely short, minute (5–7 μm) hairlike cuticular processes (fig. 168E); apical portion thus appearing dark and dull under low magnification. Shape and proportions of frontoclypeus of female and male as in figure 168C, D. Platelets of frontoclypeus very numerous, well developed, subcircular, and heavily verrucose (fig. 168I, J). Facial trichomes very short, hairlike. Thorax with platelets of dorsal portion very numerous, subcircular, glabrous, not arranged in perceptible pattern (fig. 168K). Anterosublateral setae filiform (fig. 168H). Setae of abdominal tergite II inconspicuous, very short (about 30 μm), but spinelike (fig. 168F). Tergites III and IV each with 4 + 4 short hooks (fig. 168G). Anterodorsal setae slender, spiniform. Setae of tergites V–VIII very short, length on tergite VII about 30 μm. Spinecombs on tergites VI and VII variously interrupted, especially on VI; spines of tergite VII numbering 17–18, length 10–15 μm, viz., two-thirds as long as setae of this tergite. Specialized setae of eighth and ninth segments straight or curved; branched setae not observed. Sternite V with 3 + 3, VI with 2 + 2, and VII with 1 + 1 hooks; one hook each also in pleural membrane of segments VI and VII. Sternite VIII glabrous.

Mature larva. Length 8.5–9.0 mm; width of head capsule 9.0–9.5 mm. Larva brownish, with hypodermal pigment uniformly distributed over entire body. Body shape usual

for the genus; ventral papillae well developed. Head yellow, with spots on cephalic apotome very conspicuous (fig. 168Q). Hypostomial bridge very faintly darkened. Antenna as long as stem of cephalic fan, faintly pigmented. Antennal shape as in figure 168T; ratio of lengths of segments = 1:0.7–0.8:1.17–1.28. Terminal sensillum (fig. 168S) about 5.3 times as long as wide at base. Cephalic fan with 23–26 large rays, teeth as in figure 168O. Mandible with 10–12 inner teeth and 15–21 marginal serrations (fig. 167K, M). Maxillary palp three times as long as wide at base (fig. 168P). Hypostomial teeth as in figure 168L, R. Median tooth distinctly beyond level of corner tooth apex; line connecting apex of median tooth to apex of first lateral tooth intersecting other teeth. Hypostomium with 10–14 lateral serrations and with 5–7 hypostomial setae in each row. Cervical sclerites as in figure 168M. Gill histoblast as illustrated (fig. 168U). Perianal scales extremely well developed, forming conspicuous, complete circumanal ring. Recurrent struts well developed. Proleg sclerite as shown in figure 168V. Crochet ring with 100–110 rows of 19–24 hooks each. Rectal gills not examined.

HOLOTYPE: PERU: *Lima:* Canta, valley of Rio Chillon, 3200 m, Oct. 28, 1972 (F. Blancas and P. Wygodzinsky; AMNH), male.

PARATYPES AND ADDITIONAL SPECIMENS: Same data as holotype, 1 female, allotype, 1 male, 2 females, paratypes (all reared, and with associated pupal exuviae), pupae, and larvae. PERU: *Lima:* Chacahuaro, Quebrada de Unturu, Rimac valley, 2600 m, Sept. 24, 1963 (A. Herrer and P. Wygodzinsky; AMNH), 2 pupae. *Junin:* Chacabamba, near road from Palcamayo to Junin, 3700 m, July 15, 1965 (P. and B. Wygodzinsky), 1 female, paratype, pupae, and larvae; Rio Paccha, near Huasqui, 3750 m, July 16, 1965 (P. and B. Wygodzinsky; AMNH), 2 larvae. *Cuzco:* Choco, 3500 m, Aug. 5, 1965 (P. and B. Wygodzinsky; AMNH), 5 males, 4 females, paratypes (all reared, and with their associated pupal exuviae), pupae, and larvae.

ETYMOLOGY: This species is named for Dr. Aristides Herrer, who first collected this and other Peruvian *Gigantodax,* and whose assistance and encouragement were so essential to our work in Peru.

BIOLOGY: Larvae and pupa of this species were found at high altitudes in small mountain streams and irrigation ditches, with water temperatures between 10 and 15°C. Larvae were collected on vegetation and occasionally on the surfaces of rocks. Pupae were found on the undersurfaces of watercress leaves, generally with one pupa per leaf, but mainly on the lower surfaces of stones on the bottom of the watercourse. In one instance, pupae were found on the almost vertical surface of a boulder among vegetation beneath falling water.

DISCUSSION: Wygodzinsky (1958), who first described and illustrated this species, assumed it to be *Gigantodax bolivianus* Enderlein; this hasty identification was not based on an examination of the types of Enderlein's species, and ignored the discrepancy in wing lengths: 4.6–5.4 mm in the present species, and 5.5–6.5 mm in *bolivianus* according to Enderlein. We have now seen part of the type series of *bolivianus* Enderlein and can show that *bolivianus* and the present species are distinct.

Among the most peculiar characters of *G. herreri* are the structure of the pupal gills, the small number of spinules on R_1, the elongate and conspicuously narrowed distimere apex of the male, and the large number of marginal serrations on the larval mandible.

Gigantodax cf. *herreri*
Figure 169A–E

MATERIAL EXAMINED: CHILE: *Tarapaca:* W of Putre, 3100 m, Oct. 14, 1967 (S. Coscarón; MLP), 2 pharate females, pupae. *Parinocota:* Lupica, 3200 m, Aug. 27, 1981 (Bobadilla; MLP), pupa and larvae.

The pupae are extremely similar to those of *herreri* from Peru described above, with the exception of the platelets of the frontoclypeus (fig. 169E) and thorax (fig. 169B), which have somewhat indistinct outlines, and none of which is verrucose as they are in typical *herreri.* The pharate females extracted were not preserved well enough to examine certain critical characters, such as the length of the calcipala. The fronto-ocular triangle (fig. 169C) is somewhat lower than in *herreri* from Peru and the sensory vesicle is larger

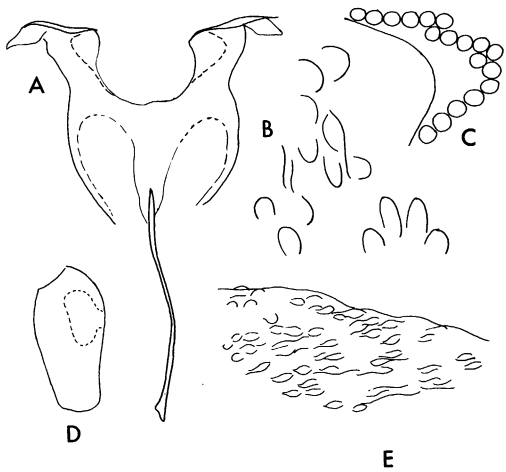

Fig. 169. *Gigantodax* cf. *herreri*. **A.** Genital fork. **B.** Platelets of thorax of pupa. **C.** Fronto-ocular triangle. **D.** Second article of maxillary palp, with sensory vesicle. **E.** Platelets of frontoclypeus.

than in specimens from Peru (fig. 169D). Until better preserved specimens can be studied, we refrain from assigning this population its definite status.

The pupae were found on the surfaces of stones.

Gigantodax impossibilis Wygodzinsky
Figures 170A–O, 171A–J, 172A–N, 173A–I

Gigantodax impossibile Wygodzinsky, 1973: 245. Vulcano, 1981: 276. Ramirez Perez, 1983: 73. [Incorrect gender]

DIAGNOSIS: Medium-size species, reddish orange imagos, with calcipala three-fourths the length of second tarsomere; pupal gill very peculiar, with two dorsal and one ventral tubular branches and anterodorsal branches subglobular; larva with median tooth longer than corner teeth.

REDESCRIPTION: *Female.* Length of wings 4.3–4.4 mm. Head dark brown; pilosity golden colored. Maxillary palp and antenna reddish brown; scapus, pedicellus, and base of first flagellomere orange colored. Scutum, scutellum, metanotum, and pleuron reddish orange; thoracic setae golden colored. Wing translucent; anterior veins orange brown, the remaining lighter colored. Setae on stem and all other veins dark. Halter yellowish white. Legs golden colored, apices of tibiae and the terminal tarsomeres darkened. Abdomen piceous, terga with posterior margins not perceptibly lighter. Abdominal hairs golden colored.

Frontal angle 45°. Fronto-ocular triangle slightly higher than wide. Shape and proportion of antennal segments as in figure 170A. Mandible with about 30 teeth (fig. 170G). Maxilla with 27–30 teeth. Last segment of maxillary palp slightly longer than penultimate (fig. 170B). Second segment of maxillary palp elongate (fig. 170D), ratio length/width = 1:0.35–0.38. Sensory vesicle comparatively short, without distinct neck (fig. 170F). Sc with 20–22 hairs. R with setae arranged in one irregular row. R_1 with numerous spinules, singly or in pairs, beginning much basal to level of insertion of Sc on C, in some cases (fig. 170E) at base of R_1. Setae of R_1 less numerous than spinules. R_s with setae in a single row on basal half, apical portion with two rows, one on convex and one on concave portion of vein. A_1 almost reaching wing margin. Shape and proportion of fore and hind leg segments as in figure 170H, I. Hind basitarsus about eight times as long as wide. Calcipala considerably beyond middle of second tarsomere (fig. 170J, K). Basal tooth of claw as in figure 170L. Eighth abdominal sternite with only delicate hairs (fig. 170M). Genital fork, cercus, and paraproct as in figure 170N, O.

Male. Length of wing 4.0–4.3 mm. Color as in female, but scutum deep orange. Holoptic. Shape and proportions of antennal segments as in figure 171A; ratio length/width of first flagellomere 1:0.45–0.50. Terminal segment of maxillary palp slightly longer than penultimate (fig. 171B). Sensory vesicle small, suboval, with distinct, short neck (fig. 171C). Sc with 15–20 setae. R with setae arranged in one irregular row. R_1 with numerous spinules, arranged singly or in pairs, beginning basal to level of insertion of Sc on C; setae of R_1 less numerous than spinules. R_s with setae as in female, some of the setae of apical half of vein almost spinulelike. A_2 almost reaching wing margin. Shape and proportions of fore and hind leg segments as in figure 171D, E. Fore basitarsus 14.5 times, hind basitarsus 6.9–7.2 times as long as wide. Calcipala as in figure 171F. Distimere two-thirds as long as basimere, with two or three apical

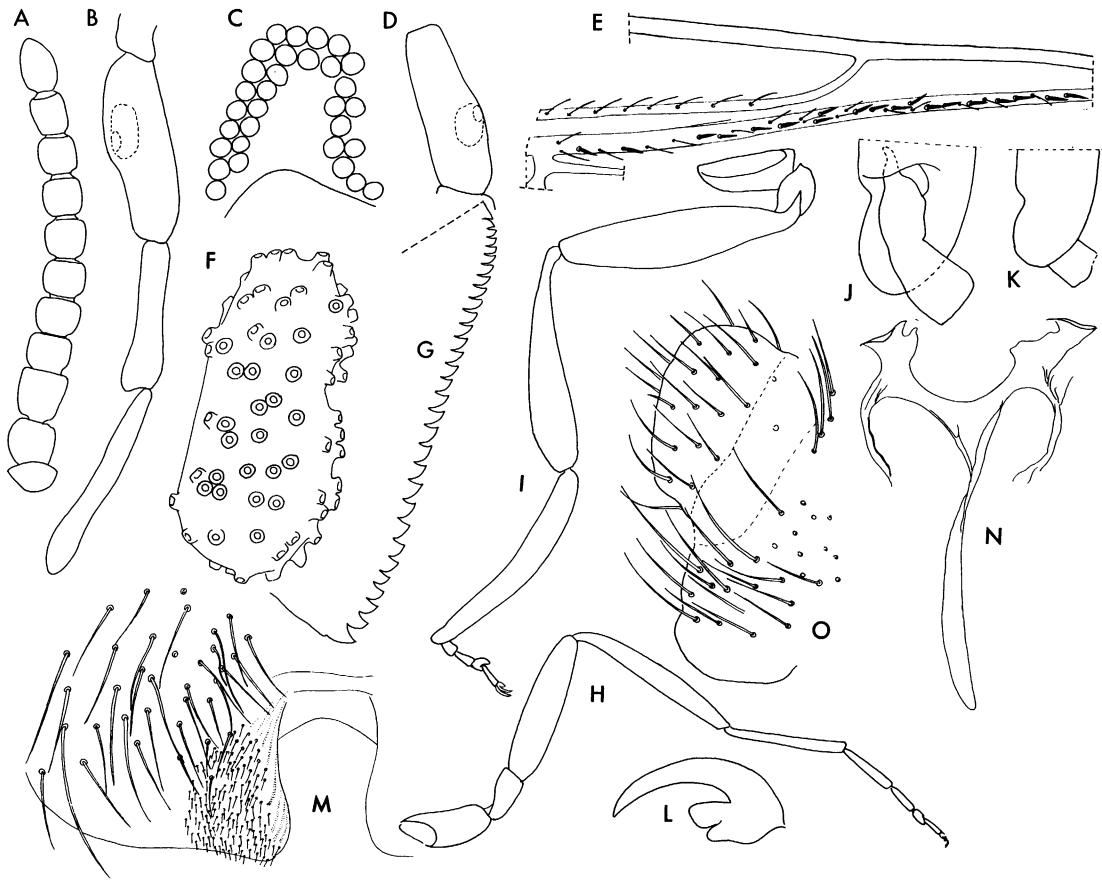

Fig. 170. *Gigantodax impossibilis.* Female. **A.** Antenna. **B.** Maxillary palp. **C.** Fronto-ocular triangle. **D.** Second article of maxillary palp. **E.** Detail of wing. **F.** Sensory vesicle of maxillary palp. **G.** Anterior border of mandible. **H.** Foreleg. **I.** Hind leg. **J, K.** Calcipala, with second tarsal segment. **L.** Claw. **M.** Sternite VIII and gonapophyses. **N.** Genital fork. **O.** Cercus and paraproct.

spines (fig. 171G, H). Main body of ventral plate as long as wide (fig. 171J). Endoparameral organ as in figure 171I.

Pupa. Cocoon conical, covering pupa to middle of anterior portion. Color of cocoon very light brown, cocoon very thin, translucent; length of cocoon along dorsum 3.7–4.0 mm. Total length of body of pupa 4.5–4.7 mm; cephalopterothecal length 2.4–2.7 mm. Gill highly modified, with four branches, two dorsal, one anterolateral, and one ventral (fig. 172B, D, G, I). Dorsal branches tubular, curved backward, slightly swollen subapically. Anterolateral branch subglobular, diameter approximately equal to width of thorax of pupa. Ventral branch tubular, distal half upward curved. Tubular branches with surface glabrous. Globular branch with basal half glabrous, apical half irregularly rugose (fig. 172E), in some specimens with remnants of two respiratory filaments. Frontoclypeus of female and male as illustrated (fig. 172A, M), with large number of faintly verrucose platelets. Facial trichomes short, spinelike. Platelets of thorax very numerous, much as on frontoclypeus, not arranged in distinct groups, slightly verrucose. Five to seven dorsocentral and dorsolateral trichomes hairlike (figs. 172N, 173A). Setae of abdominal tergite I hairlike, rather long (70–90 μm). Setae of tergite II spinelike, short, 40–60 μm long (fig. 173B). Tergites III and IV each with 4 + 4 short hooks (fig. 172F). Anterosublateral setae short spiniform (fig. 172L). Setae of ter-

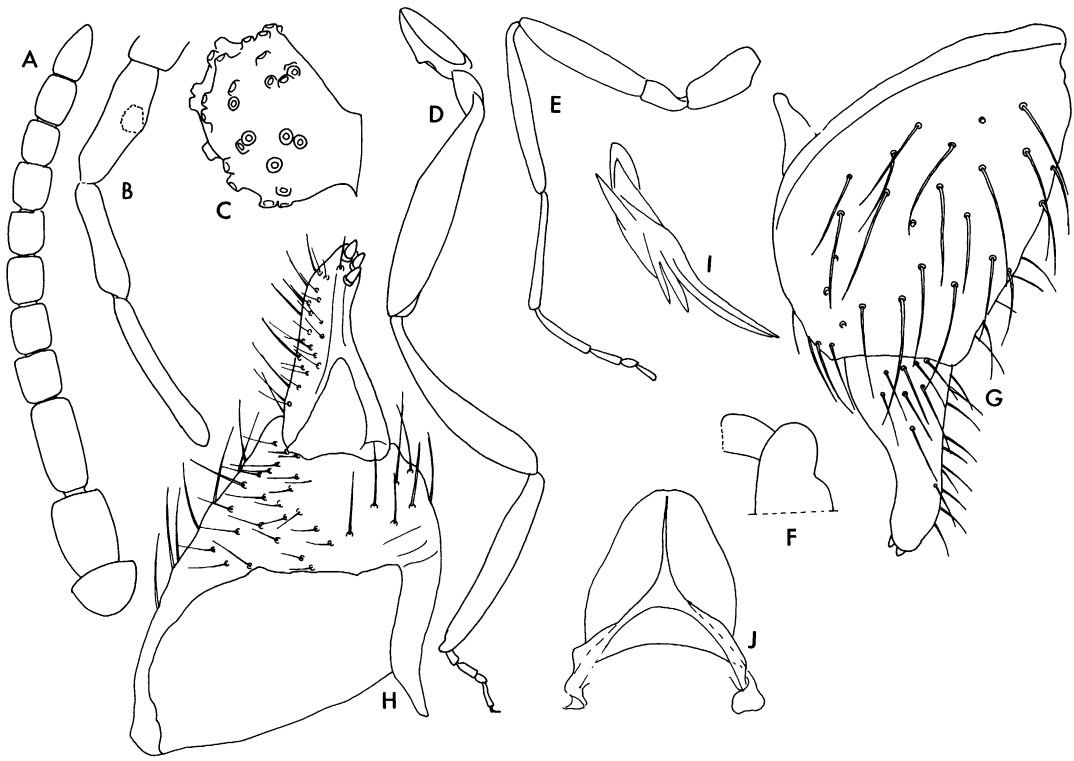

Fig. 171. *G. impossibilis.* Male. **A.** Antenna. **B.** Maxillary palp. **C.** Sensory vesicle of maxillary palp. **D.** Hind leg. **E.** Foreleg. **F.** Calcipala. **G.** Basimere and distimere, under surface. **H.** Same, upper surface. **I.** Endoparameres. **J.** Ventral plate.

gites V–VIII slender, length on tergite VII about 60 μm. Spine-combs on tergites VI–VIII, continuous or interrupted at middle, on tergite VII with about 26 spines, length 20–25 μm, viz., one-fourth to one-third the length of setae of this tergite. Specialized setae of eighth and ninth segments from straight to curved and hooklike. Sternite IV with three groups (one median and 1 + 1 sublateral) each with two small hooks (fig. 172J). Sternite V with 3 + 3, VI with 2 + 2, VII with 1 + 1 hooks; each of these sternites in most specimens also with 1 + 1 sublateral, spinelike setae; one hook and 2 + 2 spinelike setae each also in pleural membrane of segments VI and VII (fig. 172K). Sternite VIII glabrous.

Mature larva. Length 8 mm; width of head capsule 0.8 mm. Body shape usually for the genus; ventral papillae well developed. Color of larva whitish, with faint hypodermal pigment over entire body. Head light brown; spots of head capsule distinct. Hypostomial bridge lacking pattern elements. Antenna as long as stem of cephalic fan, faintly pigmented. Shape of antenna as in figure 173C; ratio of segments I–IIII = 1:0.72–0.80:1.36–1.58. Terminal sensillum slender, 4.7–5.0 times as long as wide at base. Cephalic fan with 28–32 large rays, teeth as in figure 173E, the small teeth slightly decreasing in size within each group. Mandible (fig. 173D) with 9–10 inner teeth and 7–9 marginal serrations. Maxillary palp about three times as long as wide at base (fig. 173F). General structure of hypostomium as illustrated (fig. 173G, H); apex of median tooth slightly projecting beyond level of corner tooth apex; line connecting apices of median tooth and fourth lateral tooth intersecting corner tooth. Hypostomium with seven to nine lateral serrations and five to seven hypostomial setae. Cervical sclerites as in *G. cormonsi.* Gill histoblast as illustrated (fig. 173I), showing the three tubular branches and the globular

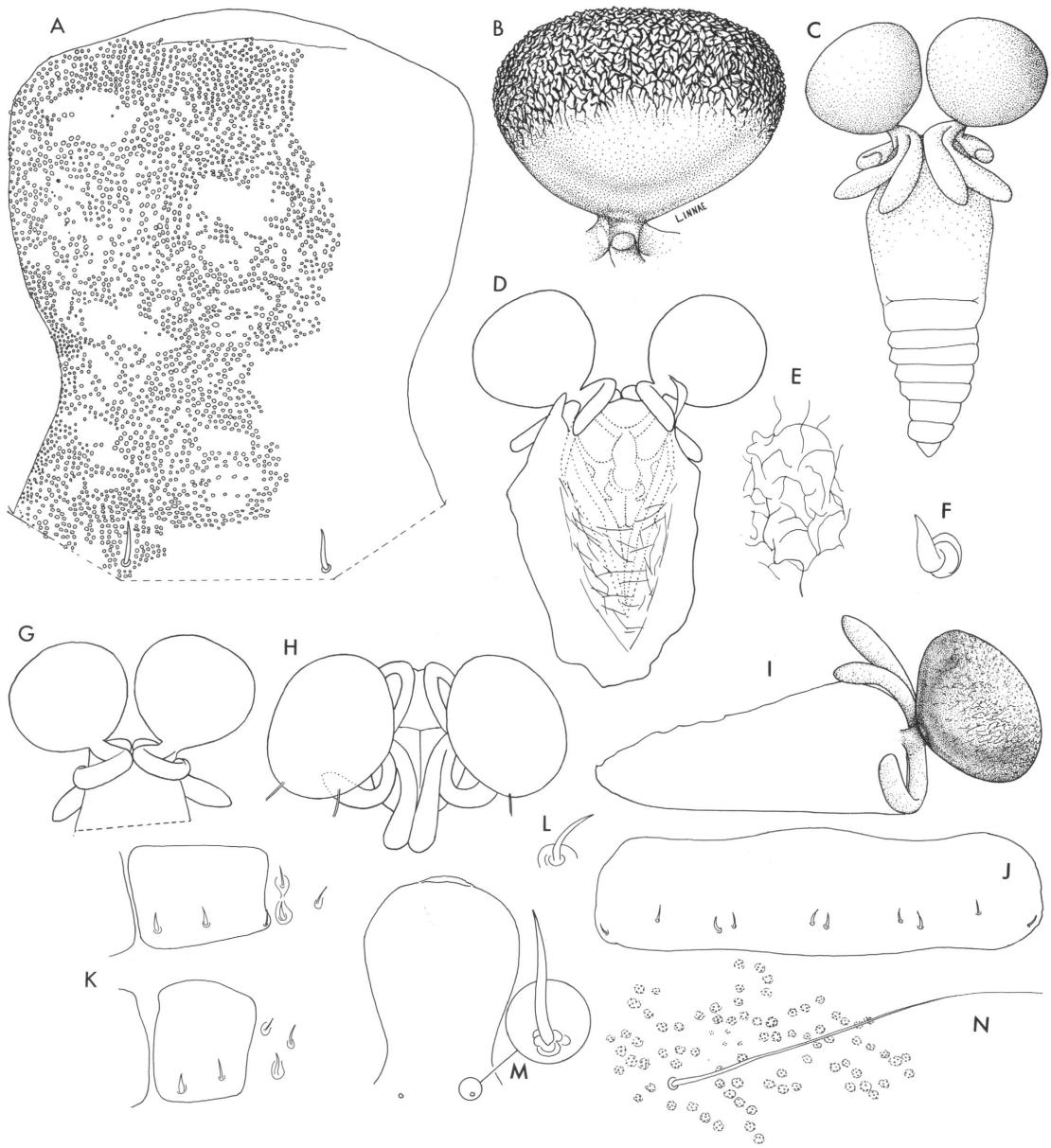

Fig. 172. *G. impossibilis.* A, B. Pupa. **A.** Frontoclypeus of female pupa with platelets. **B.** Gill. **C.** Pupa in dorsal view. **D.** Pupa in cocoon, ventral view. **E.** Surface structure of apical portion of gill globe. **F.** Hook of tergite IV. **G.** Anterior portion of body with gills, under surface. **H.** Same, frontal view. **I.** Same, side view. **J.** Sternite IV. **K.** Sternites V and VI. **L.** Anterosublateral trichome of tergite III. **M.** Frontoclypeus of male. **N.** Trichome of thorax with platelets.

branch, latter with two respiratory filaments. Recurrent struts well developed. Crochet ring with about 110 rows of 23–35 hooks each.

MATERIAL EXAMINED: VENEZUELA: *Merida:* near road from Apartaderos to Santo Domingo, 3400 m, Feb. 20–26, 1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), 1 male, 1 female, 8 males, 11 females (all reared, and with their associated pupal exuviae), pupae, and larva; Apartaderos, 3550 m, Feb. 9,

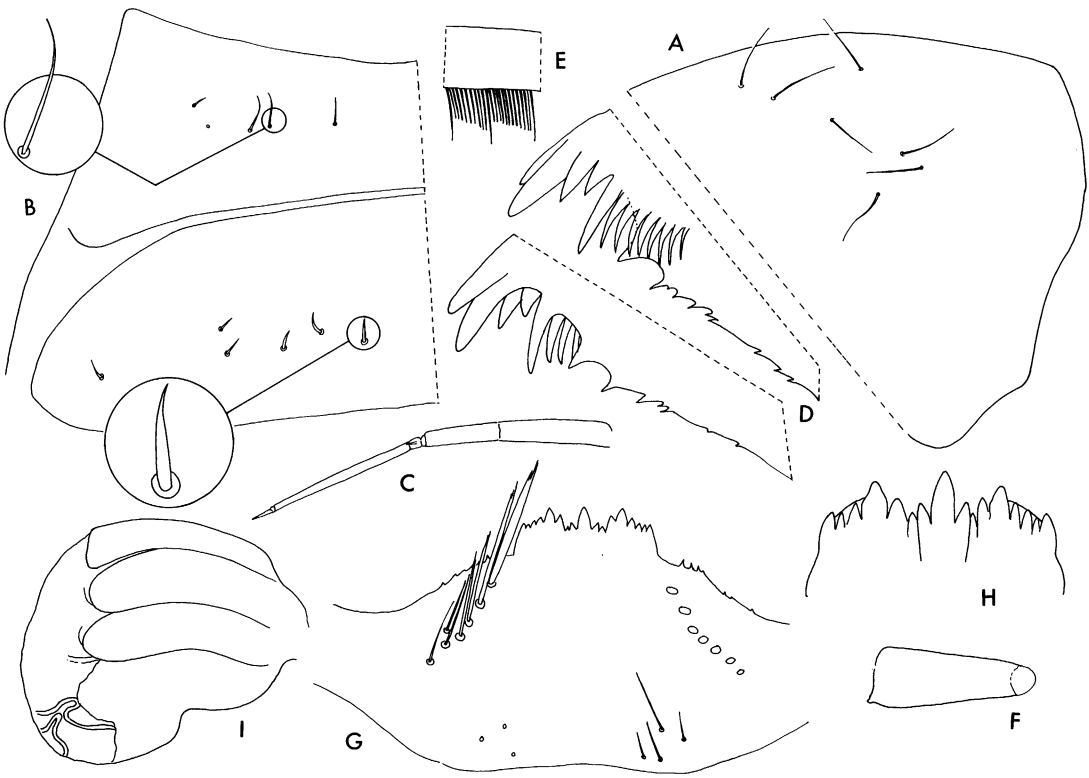

Fig. 173. *G. impossibilis.* A, B. Pupa. **A.** Chaetotaxy of thorax. **B.** Chaetotaxy of abdominal tergites I and II. C–I. Larva. **C.** Antenna. **D.** Apex of mandibles. **E.** Teeth of cephalic fan. **F.** Maxillary palp. **G.** Hypostomium. **H.** Teeth of hypostomium. **I.** Gill histoblast.

1968 (P. and B. Wygodzinsky, M. Cormons; AMNH), larvae.

BIOLOGY: The larvae and pupae of *G. impossibilis* were found on the paramos in a torrential mountain stream tumbling over boulders and with a rocky bottom; the water temperature was 15°C. The pupae were collected on the undersurfaces of rocks, mostly in shallow water near the shore of the stream. These pupae, generally occurring singly, were found together with those of *Gigantodax destitutus, Simulium bicoloratum, S. cormonsi,* and *S. jaimeramirezi.*

DISCUSSION: The structure of the pupal gills of this species is sufficient to distinguish it from all other species of the genus. Other striking characters are 2 + 2 + 2 spinelike hooks on sternite IV of the pupa, hairlike thoracic trichomes, an often high number of spines on the pupal abdomen, the comparatively long second antennal segment of the larva, the long median tooth of the hypostomium, and the comparatively short sensory organ of the palp. The color of the scutum is also quite different from those species of the *cormonsi* group.

Gigantodax cypellus, new species
Figures 174A–R, 175A–L, 176A–K

DIAGNOSIS: The cup-shaped pupal gill distinguishes this species from all others of the genus.

DESCRIPTION: *Female.* Wing length 5.0–5.6 mm. Head blackish, pilosity brass colored. Antenna and maxillary palp dark brown; scapus, pedicellus, and base of first flagellomere from light brown to orange. Scutum from light to dark reddish brown, median longitudinal area darkest, limited on each side by delicate light-colored line, a similar longitudinal line perceptible along middle. Anterior border and shoulders lighter. Scutellum and metanotum as dark as central portion of scutum. Pleural

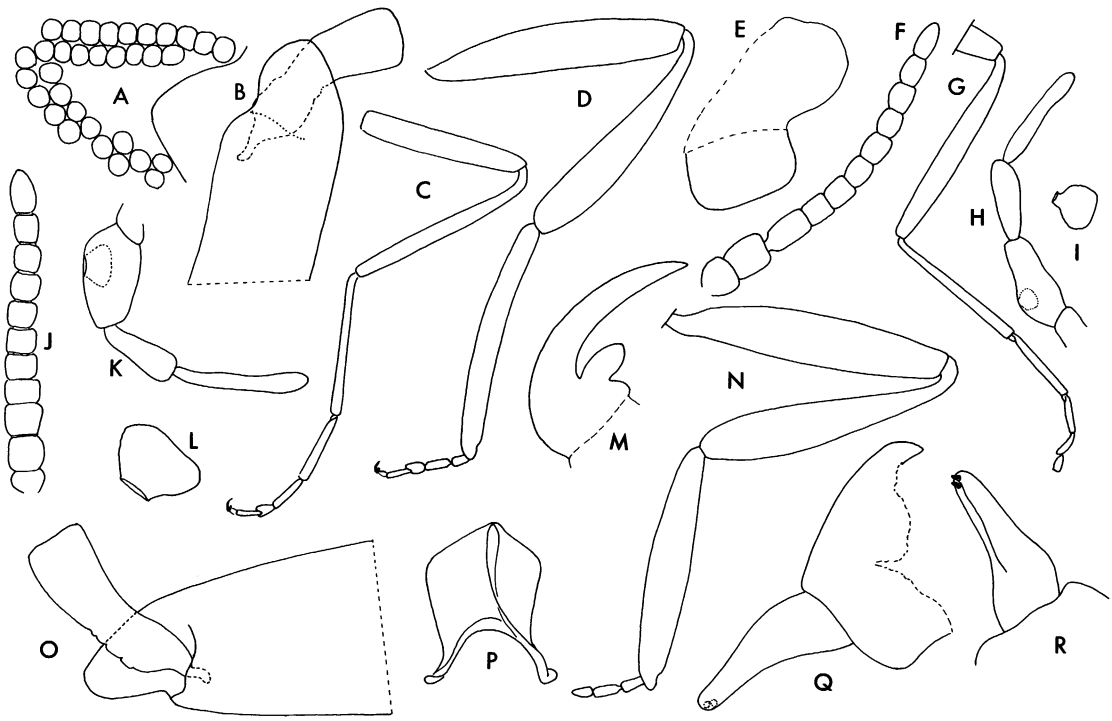

Fig. 174. *Gigantodax cypellus.* A–E. Female. **A.** Fronto-ocular triangle. **B.** Calcipala, with second tarsal segment. **C.** Foreleg. **D.** Hind leg. **E.** Cercus and paraproct. F–I. Male. **F.** Antenna. **G.** Foreleg. **H.** Maxillary palp. **I.** Sensory vesicle of maxillary palp. J–M. Female. **J.** Antenna. **K.** Maxillary palp. **L.** Sensory vesicle of maxillary palp. **M.** Claw. N–R. Male. **N.** Posterior leg. **O.** Calcipala and second tarsal segment. **P.** Ventral plate. **Q.** Basimere and distimere, under surface. **R.** Distimere, upper surface.

region reddish brown, much lighter than scutum. Thoracic setae brass colored. Wing translucent; veins light yellowish brown. Setae on stem vein dark, remaining setae of wing also dark. Halter light brown. Legs light brown, apices of femora and bases of tibiae slightly darkened; setae concolorous. Abdominal terga piceous, posterior margins narrowly bordered with yellowish white, disc of some terga mottled with yellow. Abdominal hairs brass colored.

Frontal angle 55–60°. Fronto-ocular triangle higher than wide (fig. 174A). Shape and proportion of antennal segments as in figure 174J. Mandible with 29–32 teeth. Maxilla with about 22 teeth. Second segment of maxillary palp suboval (fig. 174K). Sensory vesicle (fig. 174L) large, rather deep. Sc with 26–34 hairs. R and R_1 with setae in one or two irregular rows; spinules in R_1, beginning at level of insertion of Sc on C; R_s with setae in two irregular rows. A_2 not reaching wing margin. Shape and proportions of leg segments as in figure 174C, D. Hind basitarsus 8.9–9.1 times as long as wide. Calcipala reaching middle of second tarsomere (fig. 174B). Basal tooth of claw short, subtriangular (fig. 174M). Cercus and paraproct as in figure 174E. Eighth sternite, gonapophyses, and genital fork without special characters.

Male. Length of wing 4.8–5.1 mm. Color as in female, but scutum dark chestnut brown, practically concolorous. Holoptic. Shape and proportions of antennal segments as in figure 174F; ratio length/width of first flagellomere 1:0.60–0.65. Apical segment of maxillary palp (fig. 174H) distinctly longer than penultimate. Sensory vesicle (fig. 174H) distinctly longer than penultimate. Sensory vesicle (fig. 174I) small, subglobular, with short but distinct neck. Wing much as in female, but setae on R in a single row, and spinules on R_1

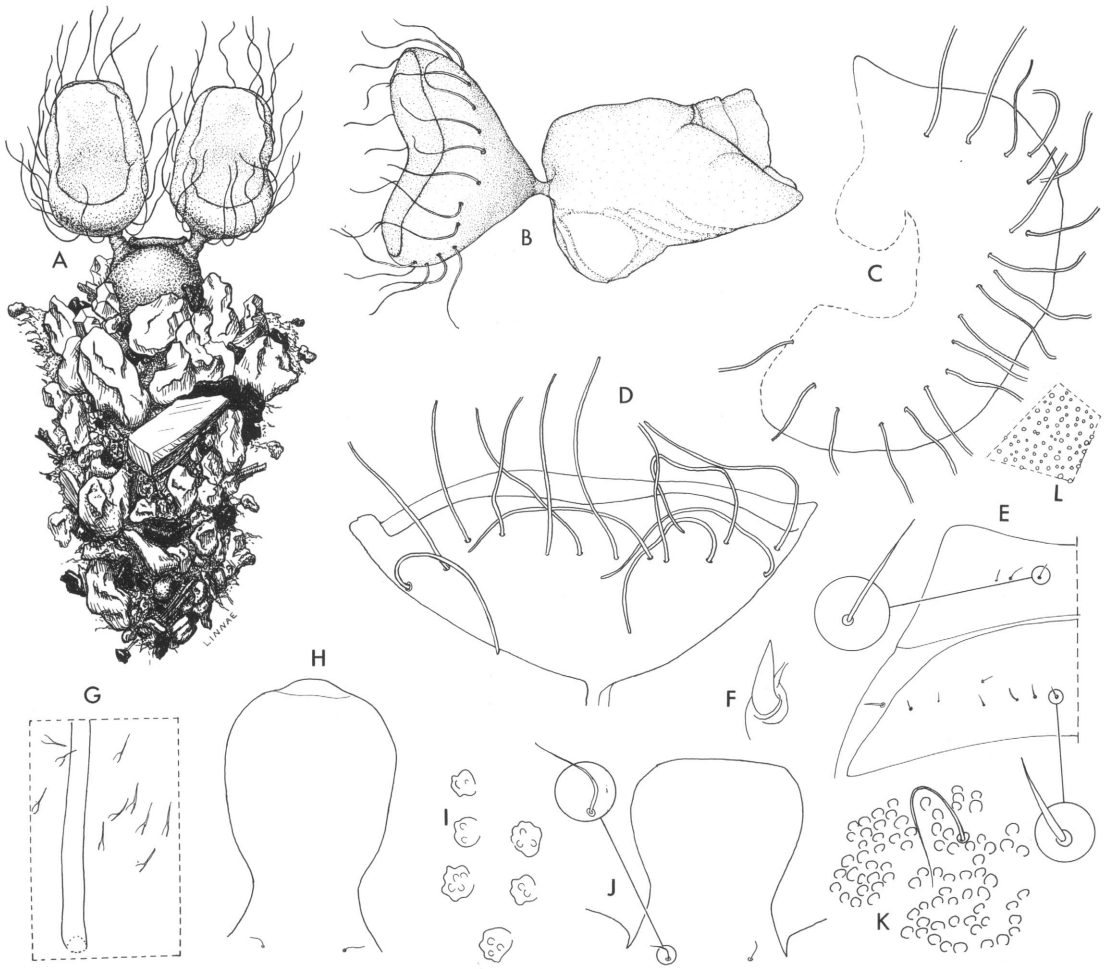

Fig. 175. *G. cypellus* pupa. **A.** Pupa, dorsal view. **B, D.** Gill in lateral view. **C.** Gill, dorsal view. **E.** Chaetotaxy of abdominal tergites I–II. **F.** Hook of tergite IV. **G.** Gill portion with insertion of respiratory filaments. **H.** Outline of male frontoclypeus. **I.** Platelets of frontoclypeus. **J.** Outline of female frontoclypeus. **K.** Trichome of thorax. **L.** Microstructure of base of gill.

beginning slightly basal to insertion of Sc on C. Shape and proportions of segments of fore and hind legs as in figure 174G, N. Fore basitarsus 15.1 and hind basitarsus 5.8–6.0 times as long as wide. Calcipala reaching middle of second tarsomere (fig. 174O). Genitalia as in figure 174P–R. Dististyle long and slender, over two-thirds as long as basimere, with two apical spines. Main body of ventral plate as long as wide.

Pupa. Cocoon small, covering pupa only to base of thorax; most of thorax as well as head and gills free (fig. 175A). Cocoon light yellowish brown, tightly woven, translucent. In material examined, cocoon thickly covered with grains of sand and other particles of foreign matter. Length of cocoon along dorsum 3.8–4.0 mm. Total length of body of pupa 4.5–5.0 mm; cephalopterothecal length 2.8–3.0 mm. Gills each with one somewhat laterally compressed goblet-shaped structure, inserted on a very short stalk (fig. 175A, B, D). The structure is entire when observed in pharate pupae but ruptures after emergence of the pupa. Height of gill 1.0 mm, greatest diameter 2.5–2.8 mm. Sides of gill with a circle of 20 respiratory filaments (fig. 175A–D). Cuticle of gill minutely dotted from

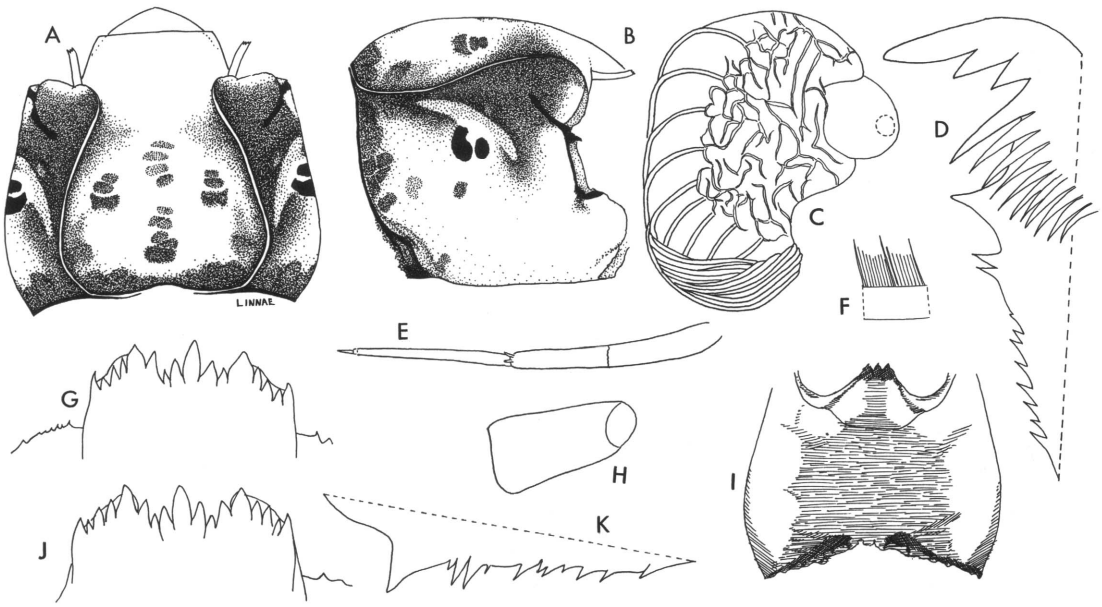

Fig. 176. *G. cypellus.* Larva. **A.** Head, dorsal view. **B.** Same, side view. **C.** Gill histoblast. **D.** Apex of mandible. **E.** Antenna. **F.** Teeth of rays of cephalic fan. **G.** Anterior portion of hypostomium. **H.** Maxillary palp. **I.** Under surface of head, with pigmentation. **J.** Anterior portion of hypostomium, different specimen. **K.** Mandibular serrations.

its base to level of insertion of respiratory filaments (fig. 175L); cuticle smooth from level of insertion of filaments to rim of calyx, but with scattered minute conical projections with filiform apices (fig. 175G). Shape and proportions of frontoclypeus of male and female as in figure 175H, J, with numerous heavily verrucose platelets (fig. 175I). Facial trichomes slender, hairlike. Platelets of thorax very numerous, not in patterns, structure as on frontoclypeus. Dorsocentral and dorsolateral trichomes of thorax hairlike, short, very inconspicuous (fig. 175K). Setae of abdominal tergite I very delicate, length 60–90 μm; setae of tergite II somewhat stouter, 50–60 μm (fig. 175E). Tergites III and IV each with 4 + 4 short hooks. Anterodorsal setae slender, spiniform. Hooks of tergite III as in figure 175F. Setae of tergites V–VIII unusually short and delicate, length on tergite VII only 40–50 μm. Spine-combs on tergites VI–VIII shortly but distinctly interrupted at center, consisting on tergite VII of 30–33 spines, length 15–20 μm, viz., from one-third to one-half length of setae of this tergite. Specialized setae of eighth and ninth segments from straight to variously curved and branched. Sternite VIII glabrous.

Mature larva. Length 8.0–8.5 mm; width of head capsule 0.8 mm. Body shape usual for the genus; ventral papillae well developed. Color whitish, with diffuse dark hypodermal pigment over entire body. Head capsule yellowish white; pigmentation (fig. 176A, B) very heavy and extensive, especially on sides and undersurface; hypostomial bridge conspicuously darkened, and hypostomium with distinct dark longitudinal band along middle (fig. 176I). Antenna as long as, or slightly longer than, stem of cephalic fan, faintly pigmented, third segment slightly darker than preceding. Shape of antenna as in figure 176E; ratio of segments I–III = 1:0.7–0.8:1.13–1.42. Ratio length/width of terminal sensillum 4.5–5.0. Cephalic fans with 24–28 large rays, teeth as in figure 176F. Mandible (fig. 176D, K) with 9–11 inner teeth and 10–12 marginal serrations. Maxillary palp 2.5 times as long as wide at base (fig. 176H). Hypostomial teeth as in figure 176G; median tooth reaching to or slightly past level of apices of corner teeth. Hypostomium with 9–13 lateral serrations,

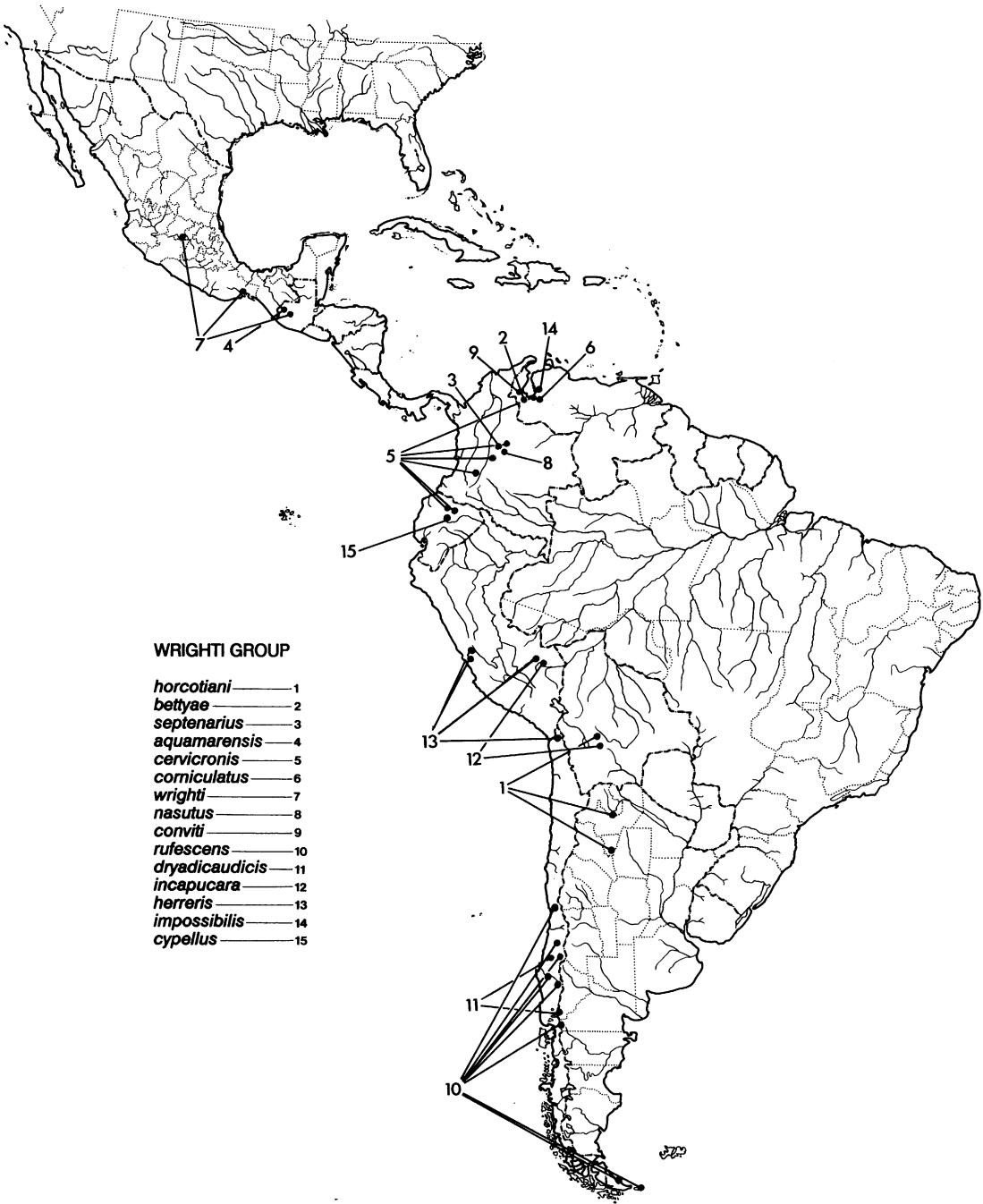

Fig. 177. Map with the distribution of species of *wrighti* group.

and 4–5 hypostomial setae in each row. Cervical sclerites as in *G. cormonsi*. Gill histoblast as in figure 176C. Perianal scales well developed, strongest and darkest near upper arms of X-shaped sclerite, forming complete though faint circumanal ring. Recurrent struts well developed. Crochet ring with 80–95 rows, each with 15–20 hooks.

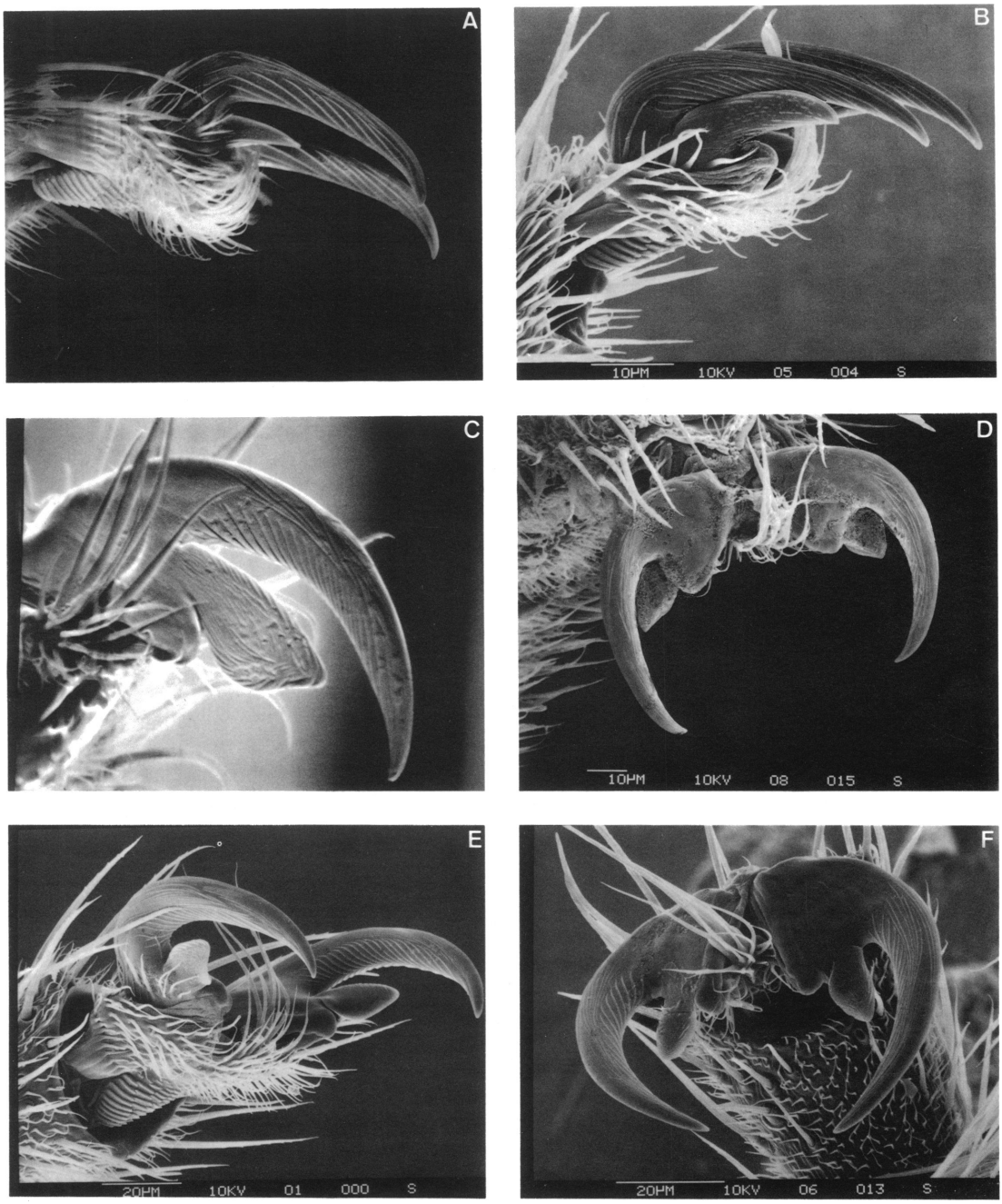

Fig. 178. Scanning electron micrographs of female claws. **A.** *G. igniculus.* **B.** *G. minor.* **C.** *G. chilensis.* **D.** *G. vulcanius.* **E.** *G. clandestinus.* **F.** *G. corniculatus.*

HOLOTYPE: ECUADOR: *Cotopaxi:* Rio Zumbahua, road from Pujili to Quevedo, 3500 m, July 29–Aug. 15, 1969 (P. and B. Wygodzinsky; AMNH), male. Paratypes and additional specimens: Same data as holotype: 1 female, allotype, 10 males, 8 females, paratypes (all reared, and with their associated pupal exuviae), pupae, and larvae; Pujili-

Quevedo road, 3600 m, July 31, 1969 (P. and B. Wygodzinsky; AMNH), pupae. *Tungurahua:* road from Ambato to Guaranda, 3500 m, Aug. 11, 1969 (P. and B. Wygodzinsky; AMNH), 1 male, paratype (reared, and with its pupal exuviae), pupae, 1 larva.

ETYMOLOGY: The name of this species is taken from the Latin *cypellum,* goblet, cup, an allusion to the cup-shaped gills of the pupa.

BIOLOGY: This species has only been collected at altitudes between 3550 and 3700 m, in clear mountain streams, at water temperatures of approximately 11°C. Pupae were in all cases found singly under rocks on the bottom of the streams. In all specimens observed the cocoons were encrusted with grains of sand, in many cases completely covering the cocoon (fig. 175A). This phenomenon was not observed in other species of *Gigantodax* collected simultaneously in the same locations.

DISCUSSION: The unique structure of the pupal gill suffices to distinguish this species from all others of the genus. The hairlike dorsocentral trichomes of the pupa recall conditions found in *impossibilis,* with which *cypellus* also agrees, in the general structure of the hypostomium of the larva. The structure of the pupal gill can well be imagined to have derived from a condition similar to that found in *impossibilis,* through the loss of the tubular branches still present in the latter, and the rupture of the globular gill of the pharate pupa upon emergence of the latter into the water. *G. cypellus* further differs from *impossibilis* by the hairlike facial trichomes of the pupa, which are spinelike in *impossibilis,* and the strong and extensive pigmentation of the larval head.

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